



Functional Morphology of Stereospondyl Amphibian Skulls

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Stereospondyls were the most diverse clade of early tetrapods, spanning 190 million years, with over 250 species belonging to eight taxonomic groups. They had a range of morphotypes and have been found on every continent. Stereospondyl phylogeny is widely contested and repeatedly examined but despite these studies, we are still left with the question, why were they so successful and why did they die out? A group-wide analysis of functional morphology, informing us about their palaeobiology, was lacking for this group and was carried out in order to address the questions of their success and demise. Based on an original photograph collection, size independent skull morphometrics were used, in conjunction with analyses of the fossil record and comparative anatomy, to provide a synthesis of the functional morphology of stereospondyl amphibians.

Stereospondyls originated in the Carboniferous and most taxonomic groups were extinct at the end of the Triassic. The early Triassic had exceptionally high numbers of short-lived genera, in habitats that were mostly arid but apparently experienced occasional monsoon rains. Genera turnover slowed and diversity was stable in the Middle Triassic, then declined with a series of extinctions of the Late Triassic. Stereospondyls showed the pattern of ‘disaster’ taxa: rapidly diversifying following a mass extinction, spreading to a global distribution, although this high diversity was relatively short-lived.

Geometric morphometrics on characteristics of the skull and palate was carried out to assess general skull morphology and identified the orbital position and skull outline to be the largest sources of skull variation. Comparing anatomy of stereospondyls with extant species revealed that the differences in head shape and orbit positions between stereospondyls allows inference of a range of feeding behaviours, ranging from rapid head swipes, to crushing invertebrates with wide palatal bones, and crocodilian-type ambushing. The range of feeding modalities meant stereospondyl species were able to coexist with minimal competition. The success was, however, short lived, as highly specialised shapes in the middle and Late Triassic probably meant that stereospondyls were not able to adapt to a more generalised lifestyle when the end Triassic extinction eliminated ecosystems.

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Chapter 1: General Introduction

1.1 Early tetrapods and the stereospondyls

As with most elements of palaeontology, the story of the evolution of the tetrapods is far from complete (Clack, 2012). It is difficult to know all of the details of how extinct species lived, even more so with an incomplete fossil record, but new fossil finds are continuously adding more information. Although the specifics of how early fish turned in to air breathing and land dwelling organisms is unknown, the overall picture is becoming clearer. The tetrapods, four-limbed vertebrates, evolved from the lobe finned fishes, and gave rise to the amphibians and amniotes (Clack, 2012). It was long assumed that adaptations for terrestrial life were a result of a land transition, first came the land, then came the legs, but this seems not to be the case. The presence of specifically aquatic adaptations, including gills and lateral line sulci show that the first tetrapods were aquatic. There is still debate as to whether the originating habitat was marine or freshwater (Clack, 2012; George and Bleik, 2011).

At the base of all tetrapods are stegocephalians, four-limbed stem tetrapods, of which the best-known genera are *Acanthostega* and *Ichthyostega* from the Devonian (Laurin et al., 2000). The clade gave rise to the amphibians and amniotes in the Carboniferous, the amniotes then gave rise to early mammals and reptiles. From here onwards the story becomes less clear, particularly amongst the amphibians. Each new character-based phylogeny produces a new topology, and the arguments about the relative position of existing and novel taxa are long and continue to this day (See Yates and Warren, 2000 and Maganuco et al., 2014). The main clades of ancient amphibians were the temnospondyls and lissamphibians. The temnospondyls arose during the Lower Carboniferous (Schoch and Milner, 2000) and a comprehensive super tree by Ruta et al., (2003) places the Temnospondyli outside of the lissamphibians, as an extinct branch of the early tetrapods. Stereospondyls were a clade of temnospondyls, which emerged in the Carboniferous. Molecular data infers lissamphibians also arose during the Carboniferous and have persisted to the modern day to include all modern extant amphibians (Marjanović and Laurin, 2007, 2009).

Stereospondyls were one of the most successful clades of early tetrapods. They dominate the amphibian fossil record of the Late Permian through Triassic with over 250 species described to date (Schoch and Milner, 2000; Benton et al., 2013, Fortuny et al. 2016).

Stereospondyls survived the end Permian extinction event, which is widely regarded as the largest mass extinction of all time (see Lucas, 2009, Frobisch et al., 2010). They existed during the entire Triassic, with additional but occasional finds from the Jurassic and Cretaceous.

Stereospondyl formed a monophyletic clade (Yates and Warren, 2000; Schoch 2013) and their gross morphology is characterised as dorsoventrally flattened crocodiliform skulls (Schoch and Milner, 2000) with weakly ossified salamander-like post cranial skeletons (Witzmann and Schoch, 2006). The skull roof and palate bones are consistent in their presence, but not shape (details of specific skull anatomy are described in Chapters 2 and 6). Stereospondyl dermal bones are easily identified by a heavily ornamented pustule and ridge pattern (Witzmann et al., 2010). The stereospondyl body plan was similar to that of a salamander but with large pectoral girdles, some had ribs with ucnate processes, and all had stereospondylous vertebrae (Schoch and Milner, 2000). A stereospondylous vertebrae is one that is completely fused (Schoch and Milner, 2000).

In addition to the impressive time and geographical distribution, the morphological diversity of stereospondyls is immense. The largest amphibians that have ever lived belong to the stereospondyls (up to 6m total body length), while the extant Chinese Giant Salamander is no longer than 1.4m (Fortuny et al., 2015). Stereospondyls ranged in size from small (a skull length of one centimetre) to large (up to six meters in total length) and showed a wide diversity of skull morphology, although post-cranial morphology seemed more conservative (Schoch and Witzmann, 2009). Skulls ranged in shape from garial-like, narrow snouted forms, to wide-headed forms with disproportionately large orbits, while others are a triangular shape. The morphological diversity also reflected an unusually varied niche occupation. They have been found in terrestrial, aquatic, marine and euryhaline deposits, from every modern day continent (Schoch and Milner, 2000; Steyer et al., 2010; Maganuco et al., 2014).

The stereospondyls are largely divided into eight taxonomic groups, though the phylogenetic assignment of groups is in constant flux and so they will be referred to simply as taxonomic groups. The synapomorphies of the groups are detailed later in section 2.3. The taxonomic groups encompass many families, genera and species, of different Epochs, niches, and locations (see chapter 3). The groups are stem stereospondyls (Schoch And Milner, 2000), Rhinesuchidae (Schoch and Milner, 2000), Capitosauroida (Schoch and Milner, 2000), Archegosauridae (Schoch and Milner, 2000), Trematosauroida (including the Metoposauridae, a family of much contention)

(Schoch and Milner, 2000), Brachyopoidea (Warren and Marsicano, 2000), Rhytidosteoidea (Schoch and Milner, 2000); and Plagiosauroida (Schoch et al., 2014). Representatives of each of these taxonomic groups feature in the analyses in this thesis.

1.2 Perceptions of stereospondyls in the literature

First described nearly 200 years ago and with new descriptions continuing to the present day (Pacheco et al., 2017), stereospondyls have been the subject of much study, from original descriptions to wider taxonomic studies. Despite this, as a group their biology is poorly understood. The reasons for the unusual morphological diversity amongst stereospondyls have been postulated, but most studies have focussed on a single species or on a family basis, no study has considered the morphology of the entire stereospondyl clade, despite its clear disparity. There is a wealth of information to be gained from a clade wide analysis of diversity, which will ultimately provide insight in to the life and death of the stereospondyls.

The literature related to the stereospondyls can be broadly split in to three categories: original species descriptions, phylogenies, and papers that feature some palaeobiology. As the literature progresses toward the present, we see more combinations of these three categories.

The earliest description of stereospondyl material was by Jaeger (1828) who reported a description of a tooth of *Mastodonsaurus giganteus* (Capitosauroida) from the Middle Triassic, although it was incorrectly ascribed to the Reptilia. A century later around 70 species had been described (Figure 1.1) but during the 20th Century the rate of discovery increased to around two species per year. There has been no plateau in the discovery of new stereospondyls in recent years (Figure 1.1).

Starting with Watson (1919) descriptions began to include attempts at descriptive phylogeny constructions and assessments of character changes. Watson (1919) was the first to group stereospondyl species into families, and consider ancestral traits for stereospondyls. In the 1960s, the species descriptions began to include some palaeobiological speculations, particularly with the works of Ochev (1966) whose works on the Russian stereospondyls included famous descriptions of Capitosauroida as “Benthic death traps”. Though with slightly less enigmatic language, more modern descriptions frequently include a phylogeny and at least a degree of speculation of the palaeobiology of the new species (Damiani and Warren, 1996; Damiani and Yates, 2003;

Damiani 2001; Jeannot et al., 2006; Fortuny et al., 2011; Marsicano, 1999; Schoch, 2000; Warrena and Marisicano, 2000; Schoch and Witzmann, 2009; Steyer, 2003; Sues and Schoch, 2013).

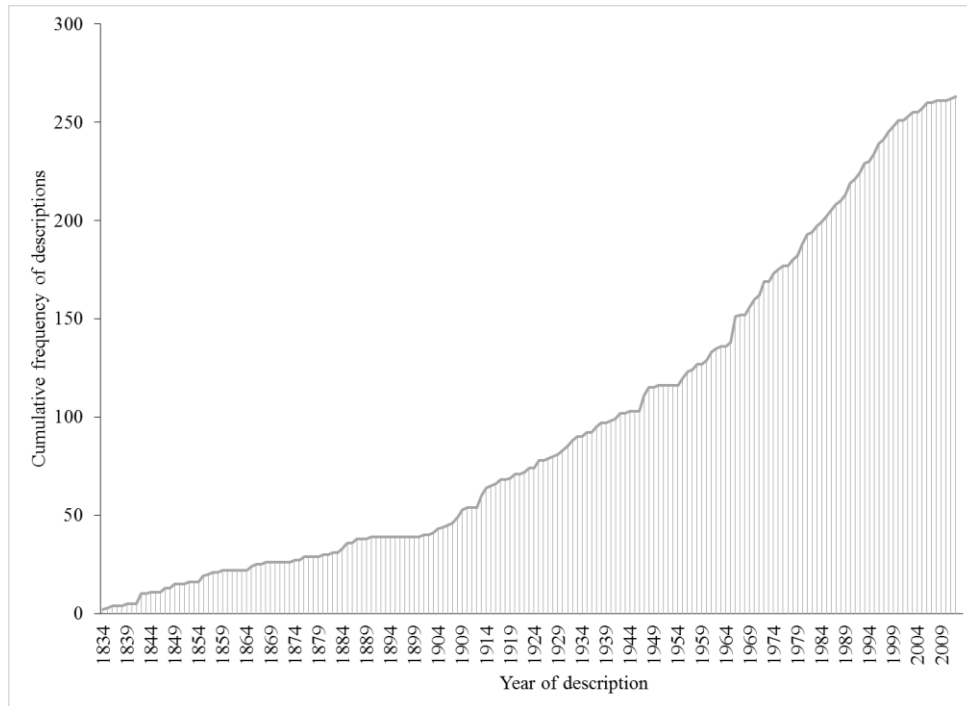


Figure 1.1 Cumulative frequency of stereospondyl species descriptions from Schoch and Milner (2000) up to 1999, and Google Scholar searches using the term “stereospondyl” and “temnospondyl” post 2000

1.3 Phylogeny

Schoch’s (2000) study of the Capitosauroida phylogeny detailed the literature history of stereospondyl taxonomic groups. Subsequent analyses by Schoch (2008), Dias da Silva and Marsicano (2011), and Maganuco et al. (2014), have dealt with other stereospondyl families and phylogenies. The papers detailed the material that had been found and described, and the conflicting phylogenies that have been presented. The changes to phylogeny, even over recent years, have been so numerous and excellently detailed by other authors, that only the key milestones will be highlighted.

The first calculated parsimony phylogeny on stereospondyls was on 12 taxa (Warren and Black, 1985) and advocated a capitosaurian group, and a paraphyletic trematosaurian group, which included the Brachyopoidea. The phylogeny was calculated by hand, so may not show the most parsimonious tree, though it was a considerable advance on the

earlier text-based discussion of relationships such as those by Watson (1919) or Cosgriff and Zawiske (1979).

Yates (1999) was the first published example of a computed phylogeny involving stereospondyls, focussing on a small family within the Rhytidosteoidea. Yates and Warren (2000) produced one of the first comprehensive computed phylogenies of stereospondyls including 32 terminal taxa, representing a range of stereospondyl species from most of the Taxonomic groups. There is a considerable advantage to the computed phylogenies, they produce multiple trees with indication of the robustness, such as bootstrap values or Bremer decay indices.

Modern (i.e. from the past 20 years) stereospondyl phylogenies, as well as those from all areas of palaeontology are constructed from the similarities and differences between species in character matrices (Yates and Warren, 2000; Schoch, 2000; Damiani, 2001; Damiani and Yates, 2003; Fortuny et al., 2011; Schoch and Witzmann, 2009; Sues and Schoch, 2013). Matrices are based on coding the characters in discrete states, producing a matrix that is subsequently analysed for the phylogeny. These characters can include any part of the skeleton that can be described in two or more states. In theory, there is no limit to the number of species or characters that can be included in a matrix since they are computed.

Damiani's (2001) review of the Capitosauroides has been used as a basis for many subsequent character based analyses because it included what was considered at the time extensive characterisation of the skull, with 15 skull roof characters, 24 palatal and occipital characters, and seven mandibular characters. There were no post cranial characters, but since these are quite conservative in stereospondyls, and postcranial remains are less frequently found than the skulls, this is not uncommon. Schoch (2013) provided a comprehensive history of the taxonomic assignments of the widest range of temnospondyls, but only included 29 stereospondyls, albeit with many more characters. Maganu et al. (2014) is one of the largest and most comprehensive phylogenies of stereospondyls, with over 100 species, though it does conflict with the superfamily concept of Schoch and Milner (2000). Although several attempts have been made to resolve the relationships of stereospondyls, it is often on a smaller scale concentrating on a family or sub-family (Damiani and Warren, 1996; Damiani and Yates, 2003; Damiani, 2001; Fortuny et al., 2011; Marsicano, 1999; Schoch, 2000; Schoch and Witzmann, 2009; Steyer, 2003; Sues and Schoch, 2013; Warren and Marsicano, 1998), or geographic

location (Damiani and Warren, 1996; Jeannot et al., 2006; Marsicano, 1999; Warren and Marsicano, 2000; Damiani, 2001; Sues and Schoch, 2013).

Some groups of stereospondyls cause particular confusion in phylogenies. The metoposauroids have been a family of particular interest because they, and the Trematosauroides, have been placed within the same clade, separated from the Capitosauroides (Witzmann and Schoch, 2006). The metoposauroids have also been placed outside of the Trematosauroides and close to the Brachyopoidea, Plagiosauroides and Rhytidosteoidea (Yates and Warren 2000). The position of the Brachyopoidea has been moved by several authors, most placing it somewhere within the stereospondyl clade (Warren and Marsicano, 2000; Yates and Warren, 2000), though others (Damiani and Kitching, 2003; Damiani and Warren, 1996) placed it outside of the clade with the Dvinosauria, but stereospondyl species were noticeably lacking from these later analyses. Schoch's (2013) phylogeny, which included both stereospondyls and non-stereospondyl amphibians, placed the Brachyopoidea within the stereospondyls.

The evolutionary history of stereospondyl families and taxonomic groups has been contested because their relationships were unresolved, initially due to lack of good material, later because of inconsistencies in phylogeny construction methods (see Yates and Warren 2000; Damiani and Kitching, 2003; Schoch 2013; Marsicano et al., 2014). The biggest challenge to understanding this large group is that no individual researcher has examined a large enough proportion of the species, so the researcher is either forced to leave species out, or to rely on incomplete literature.

A restriction of character based phylogenies, as a tool for understanding the relationships between individuals on a wider scale, is that no two published phylogenies use the same characters, coding, or taxa. Bolt and Chatterjee (2000) make an astute observation about character based phylogenies. They describe the characters themselves as "poorly stated and ... often subjective", suggesting that these cannot be reproduced by other researchers (Bolt and Chatterjee, 2000, page 679). Damiani and Yates (2003) highlighted the problem of using characters that vary with ontogeny, and the incorrect coding of characters, which can result in altered phylogenies. Schoch (2000) identified four clear problems with selection of characters for taxonomic reconstruction: individual variation, ontogeny, size correlation, and extent of ossification. This lack of consistency of character coding, whether it is opinion or error, is a challenge of these otherwise excellent phylogenies (Schoch, 2013).

Despite all of these often conflicting phylogenies, the overall picture of stereospondyls still supports the presence of several distinct taxonomic groups (Yates and Warren, 2000; Schoch and Milner, 2000; Maganuco et al., 2014). Stereospondyl relationships are only one part of their story to be told. The skulls, so heavily characterised in phylogenies, can tell us much more than who their closest relative was, they can tell us about their feeding strategies, movement abilities and visual field.

1.4 Palaeobiology

Most stereospondyl phylogenies are based on the characters of the skull and mandible, because few complete skeletons have been found (Witzmann and Schoch, 2006; Warren et al., 2011). Though frequently used in conjunction with palaeohistology, palaeoclimate, and other information, skulls have provided the basis for much of the theories about stereospondyl life-history characteristics.

Fossil amphibians that were believed to have been aquatic had more regular sculpture patterns on their skulls than their terrestrial counterparts, in particular the presence of lateral line sulci, which are deep grooves on the dorsal skull roof associated with sensory perception in water (Witzmann et al., 2010). Terrestrial living is often inferred from a “heavily ossified” skeleton (Schoch, 2013) which typically refers to the presence of a bone that is fully ossified in an adult specimen. A post-cranial bone is considered to have finished ossification when it has rounded distal ends (Witzmann and Schoch, 2006). Some stereospondyls, such as *Sclerothorxax* (a Trematosauroida stereospondyl) had a fully ossified skeleton, but also had lateral line sulci, leading to the belief that they had an amphibious lifestyle because the lateral line sulci are the location of the organs that allow detections of vibration in water (Schoch and Milner, 2000). The physical characteristics of aquatic and terrestrial environments are important in many things, for instance, locomotion. Air offers little resistance to movement but no support through buoyancy, whereas water offers support through buoyancy but creates large resistance. Different skull shapes and sizes will perform differently in each environment (Fortuny et al., 2011). Occupation of land and/or water will also bring with it a host of other ecological changes, such as prey type and availability.

Other aspects of the life-history of a species can be derived from fossil long bones. Histological examination of bones can reveal details of ontogeny and growth (Chinsamy-Turan, 2005). Histology sections of long bones showed seasonal growth cycles, identified

through lines of arrested growth (LAGs) in temnospondyl bones (Damiani, 2000; Steyer et al., 2004). Konieto-Meier and Klein (2013) suggested that bone histology can show the climate differences experienced by individuals, seasonality can be seen in periods of reduced or arrested growth, so a LAG could indicate a rainy season or cold period. There were a range of growth patterns in stereospondyls, *Metoposaurus* showed annual growth cycles (Konieto-Meier and Klein, 2013), *Duitosaurus* grew quickly and slowed down following maturity (Steyer et al. 2004), some are slow and steady, but others like *Lydekkerina* grew quickly and lived short lives (Damiani, 2000; McHugh, 2015; Canonville and Chinsamy, 2015). There was a lack of LAGs in unidentified temnospondyl femurs from Australia, though the bones were clearly striated, showing seasonal changes in bone growth (Damiani, 2000). McHugh (2015) suggested that temnospondyls of the Early Triassic show convergent evolution toward non-seasonal growth, but the assertion was based on a single sample without LAGs in the humerus of a terrestrial species of stereospondyl, *Lydekkerina huxleyi*. A closer examination of the data in McHugh (2015) actually shows that LAGs were present in most sampled stereospondyl forelimbs. The variety in growth patterns supports the disparity of life history characteristics amongst stereospondyls.

In addition to growth pattern variation, a number of well known (i.e. have many examples of the species rather than a single collection) stereospondyl genera had considerable plasticity in size and bone histology, indicative of changes in life history characteristics. *Sclerocephalus* (Archegosauridae) has aquatic and non-aquatic forms (based on the presence of gill arches and a heavily ossified pelvic girdle respectively), whereas *Gerrothorax* (Plagiosauroidea) showed different sizes and maturation rates (Schoch, 2014). The growth of stereospondyls is far from a straightforward pattern with evidence of different niches between and within different species (McHugh, 2015).

Bone histology can also give insight into locomotion and ecotypes (swimming or walking, aquatic or terrestrial). The relationship between bone microanatomy and lifestyle is well documented (Laurin et al., 2011). Aquatic species have either a more spongy medullary bone, or more compact bones than terrestrial or amphibious species (see Laurin et al., 2011). Spongy bone histology of stereospondyls supports the hypothesis of an aquatic lifestyle in some species (Damiani, 2000). Although the findings can be very useful these studies have only been carried out on comparatively few stereospondyl species.

It remains to be determined whether as a group stereospondyls were aquatic, amphibious, terrestrial, or a combination of them all. Inferring locomotion from articulated skeletons presents less of a challenge than inferring it from a skull roof alone, though skulls can provide us with a wealth of information about how these animals lived, based on principles of biology and physics. Skulls dominate stereospondyl fossil finds, thus we must consider what we can glean from these skulls to inform us of their biology. Form and function are linked to each other, and these are both linked to evolution allowing insight into fitness, selection and taxonomic change (Polly et al., 2016).

The attempts to describe skull shape across the stereospondyls have been limited to small numbers of often subjective characters. Fortuny et al. (2011) sought to determine skull weaknesses, and so bite potential, with Finite Element Analysis (FEA). FEA is a labour intensive but data rich method that has been widely applied in biomechanical analyses including tyrannosaurs (Rayfield, 2004) and extant crocodiles (Walmsley, 2013) and the Chinese Giant Salamander (Fortuny et al., 2016). Fortuny et al. (2011) identified stress distribution differences between the different stereospondyl skull shapes, which is an excellent starting point. This information needs to be built upon, incorporating more palaeobiological factors, such as orbit position and palatal features to create a more complete picture of how stereospondyls interacted with their environment. Although Fortuny et al.'s 2011 landmark paper included different stereospondyl skull shapes, it was limited to five stereospondyl species. Works such as that of Steyer (2002) and Maganuco et al., (2014) describe the biting action, in relation to head shape, but these are limited to a single species. There is a lack of a group wide analysis of objective skull shape changes in stereospondyls.

Feeding modalities are believed to be key to temnospondyl, and so stereospondyl, evolution (Fortuny et al., 2011). Different feeding modalities would naturally mean different prey types and subsequently different niches and ecotypes. The skulls of stereospondyls can give insights into their feeding morphology through their shape and anatomy. Early works described Capitosauroida stereospondyls as ambush predators who waited at the bottom of the lake or stream for prey to swim nearby (Ochev, 1966). Steyer (2003) speculated that other *Wantzonsaurus* may have been as active swimmers feeding using a side swipe biting action, inferred from a narrowed snout. Plagiosauroida stereospondyls have even been suggested to have the capabilities for suction feeding (Schoch et al., 2014), although this required very specific morphology of the skull to be

able to create the suction (Wainwright et al., 2007). However, it should be noted that these studies all lacked any quantitative or comparative analyses.

The bite of stereospondyls has only been minimally explored. In a study employing FEA simulation, maximum deformation of stereospondyl skulls was seen with a bilateral bite where force was simulated on both sides of the skull, rather than a single sided bite model (Fortuny et al., 2011). Fortuny et al. (2011) also demonstrated that stress moves in an anteroposterior direction in the stereospondyl skull, in all bite scenarios, peaking around the orbits with both bilateral and unilateral bites. A large body with a narrow snout has often been used to infer the species is an aquatic-living top predator (Maganuco and Pasini, 2009, Fortuny et al. 2011, Schoch et al. 2014). In general, species presumed to be aquatic feeders had weaker skulls and terrestrial feeders had stronger skulls characterised by short and blunt snouts and wide postorbital areas, which reduced the stress in the orbital area during a bilateral bite (Fortuny et al., 2011).

Most authors describing novel stereospondyls or reviewing stereospondyl palaeobiology have not sought to clearly determine feeding behaviours, unless there is a particular morphological feature that directly impacts the phylogeny. There are many elements that can influence feeding behaviour in these diverse amphibians, most explored in only small numbers of species. Considering the importance of feeding behaviour to ecology, it warrants further investigation across the entire clade.

The position of the nares on a medio-lateral axis has been used in some phylogenetic analyses (Schoch, 2000; Warren and Marisicano, 2000; Schoch 2008; Dais da Silva and Marisicano, 2011), as has the shape of the naris (Morales and Shishkin, 2002; Steyer 2002). The focus of these works was the relationship between stereospondyl species and not the function of the nares. There are no assessments of the position of the nares on the anterior-posterior axis, despite this being potential very informative about the function of the structures.

Several excellent in depth studies in palaeobiology in stereospondyl species exist (see Kathe, 1999; Damiani and Kitching, 2003; Damiani et al., 2009; Fortuny et al., 2011; Maganuco et al., 2014; Canoville and Chinsamy, 2015; Schoch et al., 2014. Witzmann, 2016) but none of them have attempted a clade wide analysis that incorporated objective analysis, the quality of the fossil record and comparative anatomy of a range of extant species.

1.5 Aims and objectives of this thesis

The advent of phylogeny-focussed studies has led to an increased scrutiny of the relationships between species. While these matrix-based phylogenies strive to encompass as much information as possible, they are restricted to using very few discreet characters to assess each functionally informative element of the skulls of stereospondyls. When and if palaeobiology and palaeoecology are discussed, it is frequently focussed on a small number of species and is qualitative in nature. An objective analysis of stereospondyl skull shape over time and across taxonomic groups is lacking, and in its absence, any real understanding of the reasons for their success and demise.

Clearly it is not possible to claim with complete certainty that we can determine a mode of living from fossil data alone. However, we can collect the evidence and use it to provide logical suggestions, based on what we know of physiology, physics and extant species. In my study quantitative data were collected from the widest range of stereospondyl amphibians yet studied. The emphasis is on skull morphology because of the consistent nature of fossil evidence for this structure for a wide range of species, and because post-cranial fossils are rare in this group. These data were then analysed to allow a more systematic analysis of the functional properties of the stereospondyl skull.

The aim of this thesis is to determine how changes in species diversity and morphology over time have affected the functional morphology of the skulls of stereospondyl amphibians by answering the following questions.

- How did stereospondyl distribution change over time and how is our understanding of this biased by the fossil record?
- What are the greatest sources of variability in the stereospondyl skull and does this reflect changes in lifestyles?
- Which stereospondyl groups have the greatest morphological diversity in skull features?
- What can comparative analysis with extant species tell us about stereospondyl lifestyles?

Chapter 2: General methods

2.1 Overview

This methods chapter provides an overview of the methods that apply to all subsequent chapters. How information was extracted from the literature, taxonomic affinities, and the anatomy of stereospondyls, are discussed below. The Geological Time Scale used throughout the project, the photography of specimens are also discussed. Methods and statistics that are specific to chapters are discussed within the relevant chapters.

2.2 Identifying stereospondyls in the literature

In order to have a basis for the analyses, a compendium of stereospondyls was constructed. Schoch and Milner (2000) produced an encyclopaedic volume on the clade that contained information on species name, location and taxonomic affinities which volume formed the basis of the analyses here. Schoch and Milner (2000) did not include two taxonomic groups, the Plagiosauridae and Brachyopidae, which have since been placed within the stereospondyls (Yates and Warren, 2000; Schoch, 2008). The species name, taxonomic group, geological age, anatomy, and geographical location of described stereospondyl species were recorded from the literature, to aid in the analyses of geographical and temporal distribution.

To ensure the resulting database was as comprehensive as possible, specific search terms were applied in Google Scholar, Google, Science Direct® and Scopus® (Elsevier ®). The terms were: Stereospondyl, Stereospondyli, temnospondyl, Temnospondyli, fossil amphibian. The names of each of the taxonomic groups, their sub-families and their stems, were searched for too, along with alternative spellings. For example, the terminology used in this present analysis is Archegosauridae, but the families have been known by other names, so the term “Archego” was searched as well as different spellings, such as Archegosauridae. The resulting list consists of 274 species, 50 of which are *nomen dubium* or *incertae sedis* (electronic appendix EA1). The most recent publication was used to resolve synonyms and renamed species. Not all of the species are represented in here, as this thesis is focussed on the skull roof and palate, and some species are represented by only mandible and / or post cranial material. Of the 224 certain species of stereospondyls, 129 have been used in at least one part of this thesis.

2.3 Anatomy

All measures and assessments in the analyses described in this thesis have been carried on the skull in dorsal or ventral aspect. A typical arrangement of stereospondyl skull roof and palate is shown in Figures 2.1-2.3. All figures were arranged so that the anterior is toward the top of the page, and posterior was toward the bottom of the page. Lateral and medial refer to distant-from and close-to the centre line of the skull. The arrangement of these bones is in Figure 2.3. Chapter 6 contains a more detailed description of the remaining stereospondyl anatomy.

Some features of the skull are used in taxonomic allocations and the stereospondyl skull forms the basis of the analyses in this work. The shapes of the skull characteristics that inform function were analysed to produce a picture of the functional morphology of the stereospondyls.

The stereospondyl skull roof usually consisted of 15 paired dermal bones, whose shapes and arrangement varied slightly, but was typically in the arrangement seen in Figures 2.1 – 2.2. The premaxilla, nasal, maxilla, prefrontal and lacrimal were in front of the orbit, though the lacrimal was not always visible in the skull roof of stereospondyls (Figure 2.2), it could enter the border of the naris, orbit, or neither. It has not yet been found to enter both. The frontal and jugal flanked the orbit, though their contribution to the orbital margin varied between species. The post-orbital skull comprised of the postfrontal, postorbital, parietal and the supratemporal. These suture with the bones that form the posterior skull margin, the post parietal, tabular, squamosal and the quadratojugal. Occasionally a small portion of the quadrate can be seen on the skull roof.

The premaxilla and maxilla were tooth bearing, so are exposed on the palate. The palate had an anterior palatal vacuity or fenestrae, which could be single, bilobed or double and was typically in the border between the premaxilla and vomers. The parasphenoid was the only unpaired bone in the palate and had a long thin cultriform process that separated the interpterygoid vacuities, and a base at the posterior end of the palate. The cultriform process often had a keel and terminated anteriorly well within the vomerine suture. The internal nostrils, the choanae, were in the anterior portion of the palate, frequently bordered by the anterior margin of the palatine. Posterior to the palatine was the ectopterygoid. A large subtemporal vacuity occupies the posterolateral corners of the palate, surrounded medially by the pterygoid bone. The arrangement of these bones is in Figure 2.3.

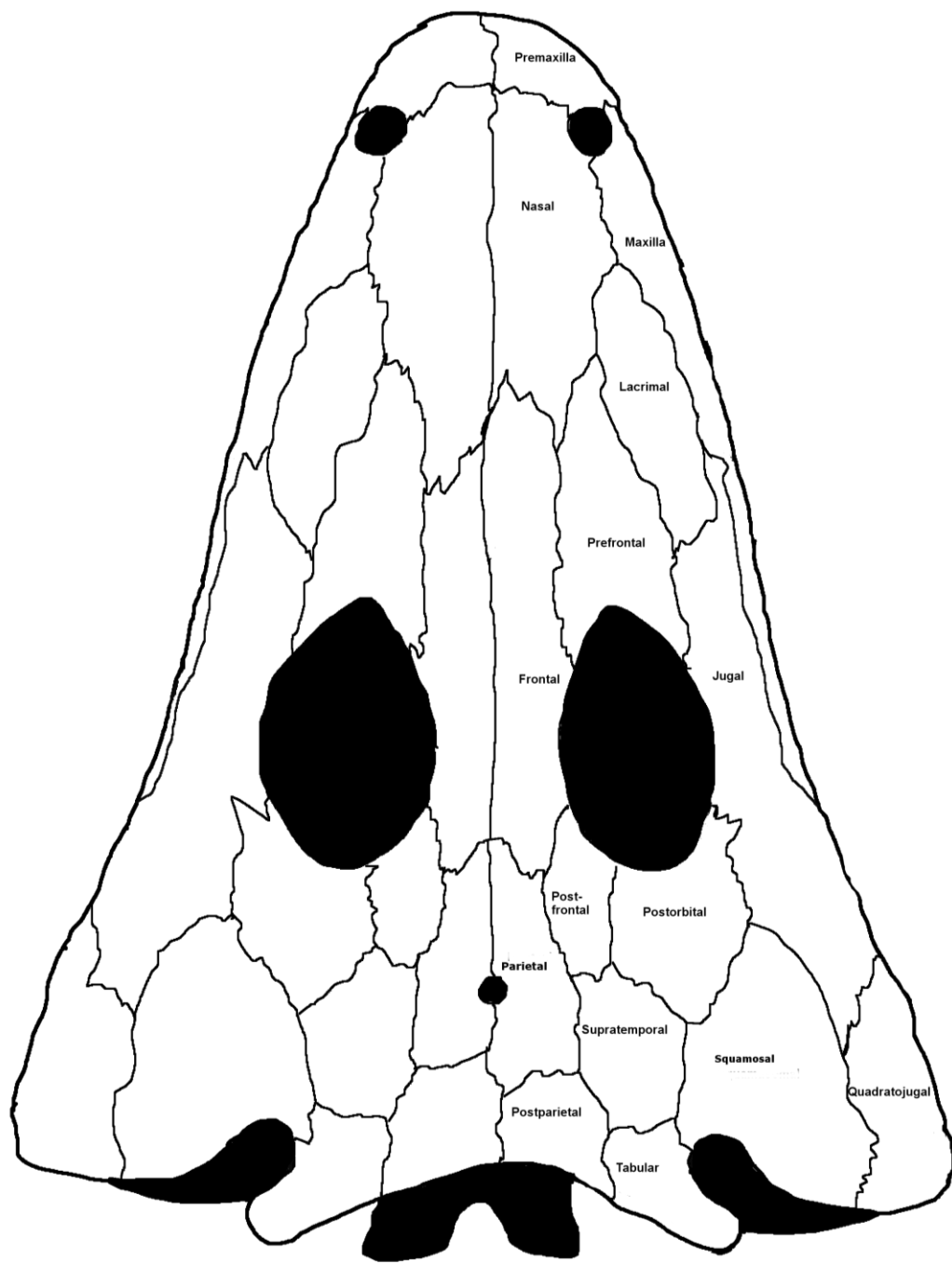


Figure 2.1 Diagram showing the skull roof of *Mastodonsaurus giganteus*, based on SMNS material (see Figure 2.3), showing a typical arrangement of dermal skull bones for a stereospondyl skull.

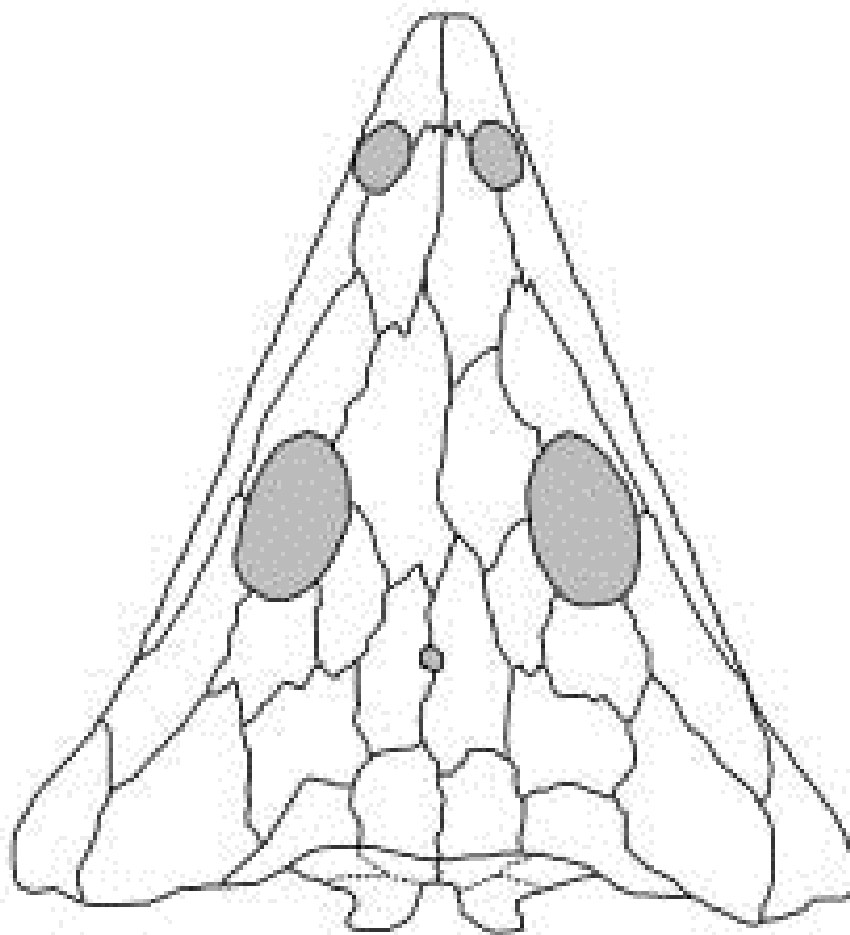


Figure 2.2 Diagram showing the skull roof of *Laidlairia gracilis* (from Schoch and Milner, 2000) with the same complement of skull roof bones as figure 2.1, except it lacks a visible lacrimal.

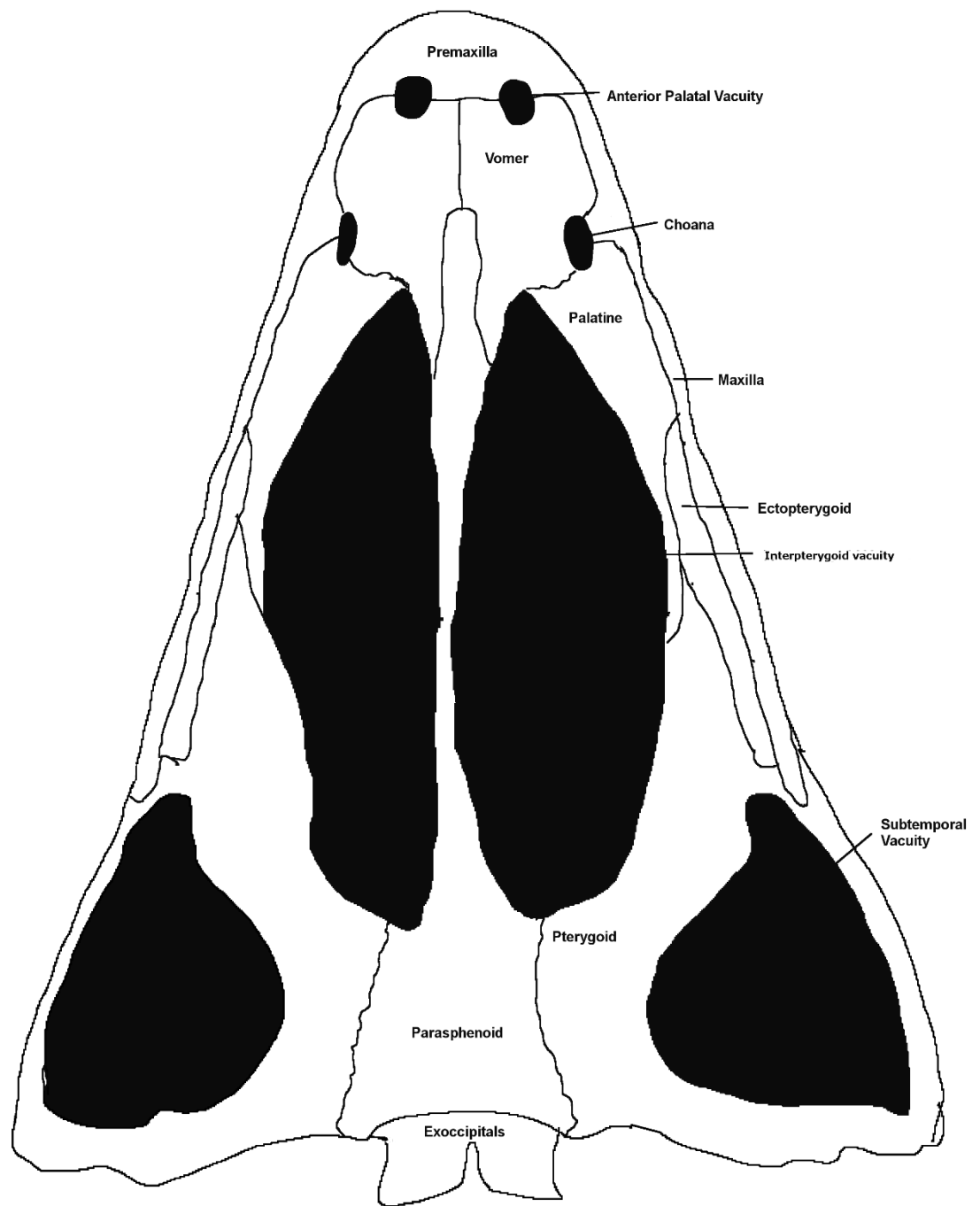


Figure 2.3 Diagram showing the palate of *Mastodonsaurus giganteus*, reconstructed from SMNS material, showing a typical arrangement of palate bones for a stereospondyl skull.

2.4 Taxonomic groups

The criterion for including a species in this work was the assignment of material to a species level and that the species be assigned to one of the stereospondyl taxonomic groups as per Schoch and Milner (2000) (Archegosauridae, Capitosauroida, Rhinesuchidae, Rhytidosteoidea, stem Stereospondyls and Trematosauroida) or Warren and Marisicano (2000) (Brachyopodea), or Schoch et al. (2014) (Plagiosauroida).

The groups included were based on taxonomic groups rather than the computed tree-based phylogenies which were discussed in Chapter 1. The taxonomic grouping approach was used by Schoch and Milner (2000) and their compendium of stereospondyls still remains the most comprehensive to date and so was used as a starting point for the inclusion of species in this analysis. Species that have been described since the Schoch and Milner (2000) publication were included where the species was clearly assigned to a stereospondyl group.

Published computed phylogenies are undoubtedly useful in the quest to understand the relationships between early tetrapods, but the analyses are often on a small number of species (eg under 50) and there is limited overlap of species between publications. Additionally, no two publications use the same suite of characters. Schoch and Milner's (2000) taxonomic group construction allowed for considerable inclusion of taxa into groups, without any further over-splitting of families and sub-families. Individual species assignments to taxonomic groups are listed in electronic appendix EA1. Where a species had been placed in different groups by authors, the paper with the most complete specimen and figured material was used as a reference for the present study. Additionally the species must have sufficient skull material to qualify for the geometric morphometric analyses (Chapter 4).

Schoch and Milner (2000) did not consider the Brachyopodea and Plagiosauroida to be stereospondyls, but Yates and Warren (2000) and numerous authors have subsequently included these two Taxonomic groups within a monophyletic Stereospondyli clade.

The sub-order Stereospondyli includes most of the large amphibians (up to 6 m total body length) from the Permian and Triassic, as well as many smaller ones (as small as 1cm skull length). The most recent comprehensive review of the group describes them as crocodiliform, with flattened skulls and bodies, exhibiting small orbits and otic notches, and with slender spiked teeth (Schoch and Milner, 2000). The synapomorphies of each group are as listed in Schoch and Milner (2000) with the exception of the Brachyopodea

and Plagiosauroidea which are described in Warren and Marisicano, (2000) and Schoch et al. (2014) respectively.

2.5 Geological time

The standard geological time scale (Cohen et al., 2014, <http://stratigraphy.org/ICSchart/ChronostratChart2014-10.jpg>) was used throughout. This timescale is produced by the International Commission on Stratigraphy and is regularly updated in the light of new information. Time periods and durations were reported in millions of years (MYr). The first stereospondyl occurrence is in the Moscovian, 315 MYrA (Schoch and Milner, 2000), and the final known occurrence was in the Aptian, 125 MYrA (discussed further in chapter 3, Schoch and Milner, 2000). A summary of the stereospondyl time range, the stage names, and start and end times is given in Table 2.1.

2.6 Image database

Specimens from eight natural history museums (see Table 2.2) were used to create a comprehensive collection of photographs of stereospondyl skulls. Data collection took place between December 2013 and March 2015.

The images were taken in dorsal or ventral aspect with a Nikon D3100 with a Nikon AF-S 40mm Macro f/2.8 DX G Lens. A scale included in the original photograph was used to set the scale prior to measurement in ImageJ (Schneider et al., 2012). Images from published literature were used in some cases, in order to represent sufficient species numbers, and were scanned from literature and size calibrated in ImageJ.

A full list of the taxa used in this study, and their sources, is in Electronic Appendix EA2. Each analysis differed, containing from 33 to 113 species depending of the availability of data for each.

Table 2.1 Time periods of stereospondyl occupation in the fossil record and their start and end time in millions of years ago.

Period	Epoch	Age	Start	End
Cretaceous	Lower	Albian	113	100.5
Cretaceous	Lower	Aptian	125	113
Cretaceous	Lower	Barremian	129.4	125
Cretaceous	Lower	Hauterivian	132.9	129.4
Cretaceous	Lower	Valanginian	139.8	132.9
Cretaceous	Lower	Berriasian	145	139.8
Jurassic	Upper	Tithonian	152.1	145
Jurassic	Upper	Kimmeridgian	157.3	152.1
Jurassic	Upper	Oxfordian	163.5	157.3
Jurassic	Middle	Callovian	166.1	163.5
Jurassic	Middle	Bathonian	168.3	166.1
Jurassic	Middle	Bajocian	170.3	168.3
Jurassic	Middle	Aalenian	174.1	170.3
Jurassic	Lower	Toarcian	182.7	174.1
Jurassic	Lower	Pliensbachian	190.8	182.7
Jurassic	Lower	Sinemurian	199.3	190.8
Jurassic	Lower	Hettangian	201.3	199.3
Triassic	Upper	Rhaetian	208.5	201.3
Triassic	Upper	Norian	227	208.5
Triassic	Upper	Carnian	237	227
Triassic	Middle	Ladinian	242	237
Triassic	Middle	Anisian	247.2	242
Triassic	Lower	Olenekian	251.2	247.2
Triassic	Lower	Induan	252.17	251.2
Permian	Lopingian	Changhsin	254.14	252.17
Permian	Lopingian	Wuchiaping	259.8	254.14
Permian	Guadalupian	Capitanian	265.1	259.8
Permian	Guadalupian	Wordian	268.8	265.1
Permian	Guadalupian	Roadian	272.3	268.8
Permian	Cisuralian	Kungurian	283.5	272.3
Permian	Cisuralian	Artinskian	290.1	283.5
Permian	Cisuralian	Sakmarian	295	290.1
Permian	Cisuralian	Asselian	298.9	295
Carboniferous	Pennsylvanian	Gzhelian	303	298.9
Carboniferous	Pennsylvanian	Kasimovian	307	303
Carboniferous	Pennsylvanian	Moscovian	315.2	307
Carboniferous	Pennsylvanian	Bashkirian	323.2	315.2

Table 2.2 Institutional abbreviations used in this thesis

Abbreviation	Institution
ESI	Evolutionary Studies Institute, University of Witswatersrand, Johannesburg, South Africa
FMNH	Field Museum of Natural History, Chicago, Illinois, USA
MB	Museum für Naturkunde, Humboldt Universitat, Berlin, Germany
PIN	Palaeontological Institute, Academy of Sciences, Moscow, Russian Federation
SMNS	Staatliches Museum für Naturkunde, in Stuttgart, Baden-Wurttemberg, Germany
UCMP	Museum of Palaeontology, University of California, Berkeley, California, USA
UMZC	University Museum of Zoology, Cambridge, England
UT-BEG	Bureau of Economic Geology, University of Texas, Austin, Texas, USA

Chapter 3: Distribution of stereospondyls in the fossil record

3.1 Introduction

3.1.1 Overview

Understanding the diversity (for example number of species) of a group is an important starting point in many studies of form and function. Although stereospondyls are now extinct, knowing something of their pattern of species diversity can provide insight into the timing and longevity of their success. Two key questions are: which times and locations were host to the highest numbers of stereospondyls? Are there any insights from the climate in the fossil record that can help us understand what was responsible for the rise and fall of these amphibians?

Some of the most interesting things about stereospondyls was their longevity through the fossil record and so several global climates, as well as their species diversity throughout those climatic periods. It is well established that climate has the potential to impact life history characteristics and ecology of species, and affect which species will be able to persist in an area (Alroy 1996, Kingsolver and Huey, 2008, Bonnet et al., 2009). Temperature in particular is explicitly linked to survival through its impact on physiology but it is also well known that body size has implications on energetics and thermoregulation (Gardner et al., 2011), especially amongst ectothermic fauna. For these reasons we should consider the environments where the stereospondyls were successful, and the species abundance in those climates could be thought of as a proxy of success (Benton et al., 2013).

Ambient temperature may not be the direct cause of a change in body size, but the secondary effect of temperature on ecosystems through prey availability and seasonality could influence life history characteristics of individuals and populations (Gardner et al., 2011). The well-known Bergmann's rule (see Gardner et al., 2011) states that smaller animals will be found at lower latitudes, hence warmer climates. Though this is based on the properties of endotherms (see Gardner et al., 2011), Kingsolver and Huey (2008) found the same pattern in ectotherms. They described it as "bigger is better", particularly within populations, and "hotter is smaller" and "hotter is better" between species (Kingsolver and Huey, 2008). Because the size effect of temperature is well known, the association of stereospondyl species diversity with palaeoclimates should be examined in this context.

Temperature is only one part of the climate, and water availability plays an important part in the environmental conditions. Rainfall patterns, water levels and river sinuosity can influence the life history characteristics of many animal species, particularly amphibians, which rely on water for at least some of their life cycle (Frobisch et al., 2010). Temnospondyl amphibians are some of the most frequently found fossils in fluvial and lacustrine fossiliferous formations (Schoch and Milner, 2000; Dias da Silva et al., 2006, Fortuny et al., 2011). The presence of water and its changes warrants closer examination, particularly amongst amphibious species that survive mass extinctions as water availability may be part of the reason for their success over the land-dwelling tetrapods.

To create a picture of stereospondyls over time, one must determine their changes in diversity over time, and consider the environments in which abundance was highest and lowest. From this, I can begin to examine the morphometric features that may be associated with those climates and how they may have aided stereospondyl success for demise.

3.1.2 Dating formations

Geological time is split into long periods (e.g. Permian, Triassic), then shorter epochs (e.g. Early Triassic, Middle Triassic), and then to more precise stages (e.g. Induan, Olenekian) (Cohen et al., 2014). The stages vary in duration, based on the presence of the upper and lower boundaries.

Most fossil finds are dated based on the location of the find in the rock strata. The formation that a fossil is found in is used to give a date range to that specimen. The dating of formations is typically based on the relative fossil finds, the presence of a plant or animal that is known only from a specific time period. On occasion, radiometric dating of volcanic sediment is carried out, but this is done on layers above and below the fossiliferous formation, and not on the fossils themselves. Unfortunately there is considerable variation between the durations of these stages (see section 3.2), that make it difficult to determine precisely how long a species was present for. In a stage lasting 18 million years a species may have survived the entire duration, or they may have only been present for one million years, in these cases there is no real way of being certain. A single fossil only gives a snapshot of one moment in time, and not precise detail of how the species survived through time.

3.1.3 The ancient world

The supercontinent, Pangea, was present in the time that stereospondyls existed. Pangea incorporated most of the landmasses of the time, and was made up of a northern area, Laurasia, and a southern area, Gondwana (see Figure 3.1). India and the southern continents were a landmass that persisted well in to the Cretaceous, which we infer from similar fossil finds in all of the continents (Carvalho et al., 2010). What is now southern Africa was close to South America when they were both a part of the continent Gondwana in the Triassic (Dias da Silva et al., 2006, Figure 3.1). To date, only two articles have attempted to identify a site of origin for the stereospondyls, both suggested a Gondwanan origin, though the conclusions were largely anecdotal (Warren and Marisicano, 2000, Dias da Silva et al., 2006). Both of these papers suggest a refuge model of recolonization, whereby stereospondyls survived the end-Permian mass extinction by remaining or retreating to Gondwana and then recolonising Laurasia, based on finds of *Rhytidosteoidea* in the Southern continents at the end of the Permian and the start of the Triassic. This concept certainly warrants further exploration, and should be scrutinised in a quantitative manner, to do it justice.

The Permian

The Permian is divided into three epochs (see Table 2.1). The Cisuralian, which is the earliest of the Permian, is split in to four ages. The two later stages, the Guadalupian and Lopingian, make up the Upper Permian with three and two stages respectively.

In the Early Permian, the southern area of Pangea was still immersed in an ice age that had begun in the Carboniferous. These glaciers receded over time and the climate became milder (Benton and Newell, 2014). It is likely that the central areas of Pangea became increasingly arid (Algeo et al., 2011). The sheer size of the Pangean supercontinent allowed for a range in extreme weathers (monsoons, deserts, high temperatures) that were a result of the large land mass and inland seas (Algeo et al., 2011, Benton and Newell 2014). There was a large intracontinental arid desert, and the tropical wet climate of the equator from the Carboniferous had disappeared (Roscher et al., 2011). Arid deserts are not conducive to the conservation of fossil material, and the size of the Permian desert means that less is known about the Permian climate than the later Triassic climate (Roscher et al., 2011).

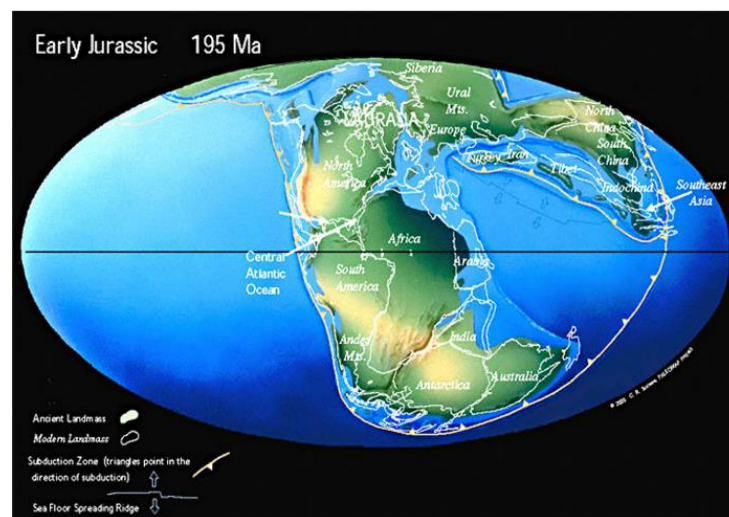
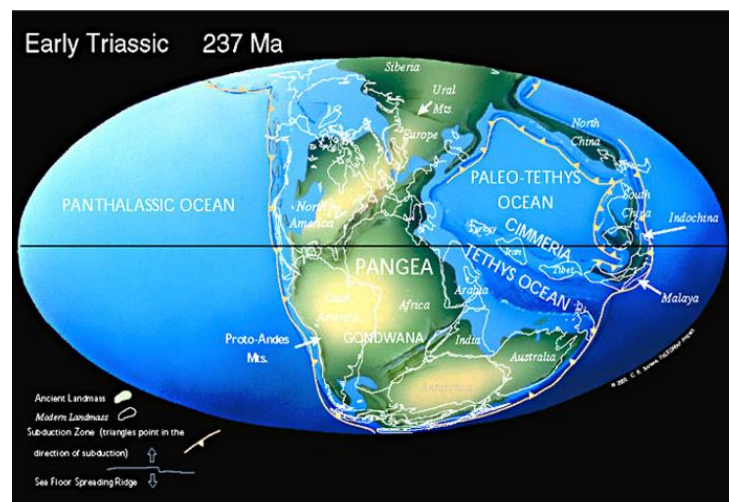
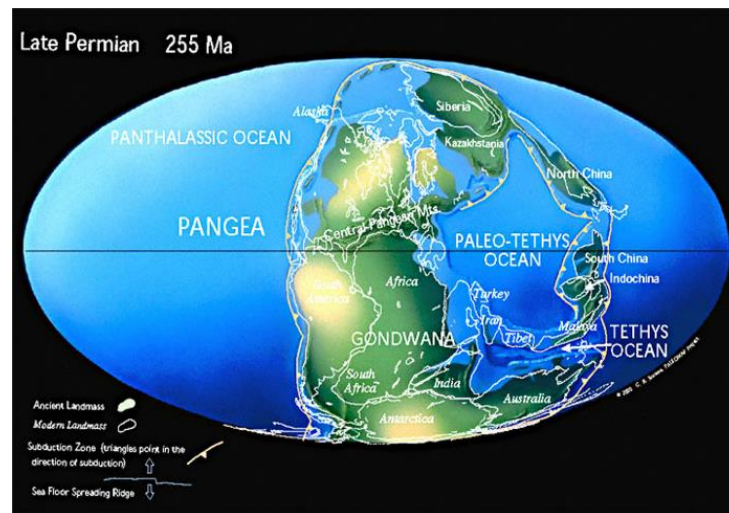


Figure 3.1 The ancient world, showing the ancient supercontinent, Pangea, with modern country boundaries overlaid, taken from the Palaeo Map Project (Scotese, 2001)

Overall global warming occurred at the Permian-Triassic boundary, confirmed by both modelling and stable isotope analysis (Roscher et al., 2011; Benton and Newell, 2014). Global warming at the end Permian may have caused shallow sea temperatures to increase by up to 8°C (Benton and Newell, 2014). The Permian-Triassic boundary is placed at 253 million years ago (MYA), following an extinction event that lasted between 100,000 and 200,000 years (Smith and Botha-Brink, 2014). Oceanic temperatures and acidity levels greatly increased at the PTB, shown by increased $^{187}\text{Re}/^{188}\text{Os}$ (Georgiev et al., 2011), resulting in what is considered the largest mass extinction in history (Roscher et al., 2011). A temperature increase of this magnitude could have created an entirely new challenge for amphibian survival.

The Triassic

The stereospondyl clade survived the end-Permian extinction and were present throughout the Triassic (Schoch and Milner, 2000). The Triassic climate is better studied than the preceding Permian as increased rock availability (and accessibility) for this period has allowed for a closer examination of the climate. The Early Triassic ecosystems had higher temperatures and fewer forests than the Permian (Benton et al., 2004). The two stages of the Early Triassic, the Induan and Olenekian, were characterised by high temperatures, fluctuating rainfall and varied levels of CO_2 (Metcalf et al., 2013). The shallow marine environments shifted between oxic and anoxic conditions over a relatively short time (Metcalf et al., 2013), making them an inhospitable environment in the Early Triassic.

The early and Middle Triassic ecosystems lacked forests and corals, evidenced by a “coal gap” in the stratigraphy. Their loss reflecting a loss of habitats and ecosystems (Benton and Newell, 2014). Erosion can be delayed by well rooted vegetation (Ward et al., 2000), so this loss of forest would have affected more than those species living in the forest. Modern deforestation is linked to erosion and loss of clarity in fluvial systems, affecting the water quality for those species that use the river in their life cycle (Ward et al., 2000; Benton and Newell, 2014). When coupled with strong monsoonal climates (Preto et al., 2010) river systems widened and straightened, with larger drainage systems (Ward et al., 2000; Benton and Newell, 2014). The loss of vegetation has been suggested as a cause of decreased river sinuosity in the Karoo Basin of South Africa (Ward, et al., 2000). All of these factors significantly altered the water topology of the Early Triassic.

The Karoo Basin became increasingly dry in the Early Triassic (Pawley and Warren, 2005). In contrast, the northern climates of Germany experienced an increase in water levels in the Early Triassic, particularly high levels in freshwater lakes (Benton and Newell, 2014). North Germany had lacustrine environments in the Permian that persisted into the Triassic (Benton and Newell, 2014). However, the Russian Ural Mountains have a PTB succession, showing a cessation in mountain development and an increase in aridification, with reduced vegetation (Benton et al., 2004), much like the Karoo. Again, similar to the Karoo, there was an increase in river channel width during the Triassic in the Ural area (Benton and Newell, 2014).

The Middle Triassic, consisting of the Anisian and Ladinian stages, was more humid than the Early Triassic, and more stable (Preto et al., 2010). It lacked the strong monsoonal fluctuations and arid areas of the Early Triassic. There was an overall decrease in global temperatures in this time. The geography also altered from the Permian through the Triassic as the Tethys sea encroached into Pangea (see Figure 3.1) (Roscher et al., 2011; Benton and Newell, 2014), which broke up the large landmass of the continent (Figure 3.1).

The first stage of the Late Triassic is the Carnian, which was characterised by an increase in rainfall (Preto et al., 2010). The Late Triassic had strong monsoonal weather, with a zonal climatic pattern (Preto et al., 2010). A pluvial (humid) phase in Europe has been suggested by some as a cause of high turnover of species at the end Carnian (see Lucas and Tanner, 2015). Atmospheric carbon dioxide levels steadily increased toward the end of the Triassic, eventually reaching double their level at the boundary (2000-2500 ppm), roughly 200 million years ago (Steinthorsdottir et al., 2011). At present they are approximately 400 ppm (Dlugokencky, 2016). The Central Atlantic Magmatic Province (CAMP) eruptions caused fluctuating cooling, warming and acidifications, but these were on a local scale (Lucas and Tanner, 2015). So the Late Triassic was peppered with local extinction events that, when viewed collectively, were seen as a mass extinction (Benton et al., 2013, Lucas and Tanner 2015). Stereospondyls have only been found at two points after the end of the Triassic (discussed in detail in a later section), so this clearly warrants a closer examination to find out why they lost their global presence.

3.1.4 Importance of distribution in the fossil record

In conjunction with knowing the palaeoclimate, it is important to know which of the geological stages hosted the greatest, and smallest, numbers of stereospondyl species and how these compare with the palaeoclimates and non stereospondyl species. From this it is possible to gain insight in to which climates were most suitable for stereospondyls and how these were associated with particular morphologies. The way the fossil record can be biased by a multitude of factors including but not limited to researcher effort, size bias, types of rock formations and their availability (discussed further later) must be considered. With this in mind the information can infer which forms were most successful in particular environments. Equally important is the rate at which species appear and disappear because disaster taxa – those which are present following a mass extinction - tend to be short lived, and some species struggle to establish themselves in new areas, particularly carnivores like stereospondyls (Abrams, 1998; Ronce, 2007).

The geographic locations of fossil finds provide some insight into the ranges of the stereospondyls. In the Early Triassic, amphibians showed large spatial differentiation, larger than the non-amphibian tetrapods present at the time (Shishkin et al., 2006). We can also tell from the fossil record whether species are globally or locally uniformly distributed for example, the Early Triassic Russian platform showed considerable tetrapod heterogeneity (Shishkin et al., 2006) an indicator of a varied and well established ecosystem (Thébaud and Loreau 2005.), though it is a well sampled area. The locations of fossil finds may also give some indication of refuges and the direction of expansion across the continent through a dominance of a location in the fossil record. As such the fossil record can help to provide an overall picture of the pattern of movement of stereospondyls, which can later be combined with functional morphology to infer their interactions with their environment.

The fossil record can provide a wealth of information on the balance of species within ecosystems of palaeoenvironments. Throughout the Permian, terrestrial amphibians were replaced by amniotes as the dominant terrestrial species (Fortuny et al., 2011). Not every group experiences a change in diversity at a major time boundary, the fossil records of insects and freshwater fish suggest no change in diversity across the Triassic – Jurassic boundary (Lucas and Tanner, 2015). The diversity of stereospondyls in these time frames and environments can give us some indication of how they were influenced by the changing environments.

The biological concept of species, which relies on the production of fertile offspring, cannot be applied to fossil finds (Benton and Pearson, 2001). In palaeontology it is widely accepted that morphology is the main criterion for species allocation, small alterations in morphology may be assigned to new species, but in reality may have been a different morphotypes of the same species. Benton (2008) identified a trend amongst dinosaur palaeontologists, those naming dinosaurian species before 1950 were less likely to have species that were still valid today following many decades of thorough scrutiny of the species morphology. It could be simply due to the keenness of the researchers to name new material. One straightforward buffer against these errors caused by small differences in morphology is to use genera diversity, rather than species diversity, with the belief that the morphological disparity between species is smaller than that between genera, so the latter is a more robust measure (Benton et al., 2013). Though there is the risk that some detail may be missed, it does mean that the foibles of an over-excited researcher assigning a new species, based on insufficient evidence, can be mitigated. It would be a very significant job to attempt to validate all stereospondyl species, particularly as some now only exist in paper form. Destruction in wars and theft mean that only original descriptions exist for several species, and since most of these descriptions were before the advent of digital photography, it would be impossible to truly validate or discard them.

Conflicting arguments exist for the role of extinction in diversification. Alroy (1996) argued that extinction is a less controlling factor than origination, as the duration of niche occupation by a taxon is a suppressor of origination, and not rapid niche occupation following an extinction event. Alroy (1996) tested the coordination stasis hypothesis on turnover of North American mammal species and found it to be poorly supported. More recently, Ruta et al., (2011) found that extinction events preceded high rates of evolution. Since the stereospondyls had such longevity through the fossil record it would be prudent to closely scrutinise the fossil record to extract as much information about genera longevity as possible.

Speciation and extinction events can provide insight into successful and unsuccessful forms in the fossil record, as does establishment success. High numbers of extinctions may indicate that a form was vulnerable to a particular climate event. High numbers of originations may indicate that there was little competition between species. Extinction events can be hidden within overall turnovers; the total number of genera can be constant, but the turnover of genera can be high (Lucas, 2009). However, a close examination of the genera within the fossil record can reveal composition changes over time. These can

be detected in the fossil record by determining the first and last occurrences of a genus in the fossil record (Alroy, 1996; Ruta et al., 2007). Stereospondyls have been included in counts of tetrapods but never examined in their own right.

It is well accepted that the end Triassic extinction was a series of smaller, localised extinction events over a longer time (Benton et al., 2013). The Late Triassic had lower origination rates than extinction rates for most species, which eventually manifested in to the Late Triassic extinction (Lucas and Tanner, 2015). Whether the largest amphibians of all time, the stereospondyls, followed this same pattern, is yet to be determined.

Patterns of diversification in the fossil record are contentious (Benton et al., 2013). The principle argument is that a literal reading of the fossil record can lead to biases caused by sampling proxies, such as rock availability, researcher effort, and the completeness of the fossil material. These biases are the focus of many research articles and do warrant a brief overview, but the aim here is not to provide a new approach, when so many already exist. Tetrapod bearing formation numbers, fossil completeness and stage duration will all be examined to infer the effect they have on the stereospondyl fossil record.

Models that seek to correct for sampling proxies do exist, but Lloyd (2012) and Benton (2015) argue that 1) there is a risk that the main trend that is removed by the model is not entirely biased and 2) the residuals (the basis of the model output), likewise can involve bias, so they are not without their own problems. These two problems, with an attractive model method, could be of minor importance and be correctable (Lloyd, 2012) or could be fatal, rendering the method meaningless (Benton, 2015). Further, formations alone are hardly a meaningful indication of sampling because they are elastic, varying in volume (i.e. rock accessibility) over eight orders of magnitude (Benton et al., 2013). It is far better to use a metric that is independent of fossil accumulation through research time and that is itself regular (analogous to the famous sampling quadrat in ecology), such as rock exposure area or rock volume, or tetrapod bearing rock formations as originally recommended for such palaeodiversity correction (McGowan and Smith 2008, Benton et al., 2013). Although rock availability and exposure are undoubtedly excellent proxies for assessing bias, the data needed are not available on a global scale, unlike tetrapod bearing fossil formations (Benton et al., 2013). Tetrapods bearing rock formations are those formations which are known to hold tetrapods and so by virtue are areas that were at some point suitable for habitation by tetrapods. This limits the extent of “empty space” where stereospondyls are absent, and so where they never would have been found such as deep sea formations.

Taxonomic biases and other foibles of the fossil record mean that using absolute counts may not yield the most reliable interpretation. However, the relative changes in diversity are quite robust against these biases and where cases of correlation exist between a proxy and diversity they can be used to identify deviations from predictions and so an assessment of diversity can still be inferred (Irmis et al., 2013).

The aim here is to identify and report the distribution of stereospondyls in the fossil record and to briefly assess potential biases in their fossil record. The time, duration and locations of genera will be discussed in light of these biases to shed some insight in to stereospondyl distribution.

Hypotheses

Stereospondyls have an equal distribution in the fossil record across time and location and so there was no association of morphotypes with climates.

Stereospondyl genera persist in the fossil record for equal lengths of time implying equal success for morphologically different groups.

The stereospondyl fossil record is not biased by stage duration, fossil completeness or tetrapod bearing fossil formations.

3.2 Methods

3.2.1 Overview

The aim here was to identify the distribution of stereospondyls in the fossil record and to see how this distribution changed over time and with geographical location whilst accounting for potential sources of bias. All species identified here have been positioned within the wider Stereospondyli or are considered stem Stereospondyli (Schoch and Milner 2000).

Species names and the location and age of their associated formation were extracted from the literature (as defined in chapter 2), to create a picture of known stereospondyl distribution in the fossil record. Some proxies were analysed with stereospondyl diversity, and with each other, in order to reveal potential biases in the fossil record. Measures of diversity are reported here as: 1) number of genera present in a stage; 2) number of originations in a stage; and 3) number of extinctions in a stage. These indices were used

to achieve an overview of the distribution of stereospondyls in the fossil record so that a record of stereospondyl diversity across time and place could be created.

3.2.2 Data

A database of stereospondyls and stem stereospondyls was assembled from the literature, as per the criteria in Chapter 2. The resulting dataset consists of 253 (excluding *incertae sedis*) species and 173 stereospondyl genera, giving a species: genus ratio of 1.4. The geographical and stratigraphic locations, the type of material described, and the first and last occurrence (stage) were recorded.

Information from the literature was cross-checked with the Early Tetrapod Database (ETD, Benton et al., 2013), particularly for the material described, where there were discrepancies then the most recent publication was used. Where possible, these entries were also checked against the Palaeobiology Database, particularly to update formation dates (PBDB, fossilworks.org) but not all stereospondyls are in the publicly maintained PBDB.

The standard geological time scale was used (Cohen et al., 2014; <http://stratigraphy.org/ICSchart/ChronostratChart2014-10.jpg>) to assign taxa to stage. The options for time bin allocation were stage or epoch. Some groups of fossils, such as the dinosaurs, have been dated to a precise time, but that information is lacking for the stereospondyls. The stage allocation was the occurrence of genera in a stage. The stages used here ranged in duration from 0.97 million years (MYr) to 18.5 MYr (Induan and Norian respectively; see Table 2.1). It started with the first known stereospondyl occurrence, the Moscovian (315 MYrA), the last known stereospondyl occurrence was in the Aptian, 125 MYrA, but as this occurrence was after a 57 million year gap in the fossil record, the analyses carried out on these data are limited to the Toarcian, 182.7 MYrA, to prevent severe skewing of bias analyses.

The degree of completeness of the specimen was used as a measure of the quality and quantity of fossil material that had been assigned to a genus and was measured on a scale of 1-4, as suggested by Benton et al., (2013): 1- One element, or a number of disarticulated elements, 2 - One or more complete skull(s), 3 - One complete skeleton, 4 - Several complete skeletons. If a correlation existed between completeness and diversity, it might suggest that many species were named on the basis of poor quality material. Each genus was allocated to one of these categories and then the mean completeness for each

stage was calculated. Though other values of central tendency were considered, the aim was to create a basic picture of the stage as a whole, and not the midpoint of completeness or the most common completeness metric and the values assigned to the data were not erroneous which allows for the use of the mean. This informal, simple metric of fossil completeness was chosen over the more detailed metrics that are based on assessment of each skeletal element (e.g. Mannion and Upchurch, 2011). My approach allowed for all genera to be included in the analysis irrespective of the specimen completeness. In order to carry out some analyses, it would require a complete count of the individual samples attributed to a species, as in Nicholson et al., (2015), which is not possible with stereospondyls. Although some museums such as University of Cambridge Museum of Zoology, have detailed collection records online, many others do not even have a computer record of their collections. It would not be possible to accurately assess the number and completeness of each of these samples in this timeframe. As the digital record of stereospondyl occurrences is patchy and inconsistent, the straightforward metric used here (and by Benton et al., 2013) meant that it was applicable to all stereospondyl genera that have been mentioned in the literature, not just those that are particularly well known or at museums with digital archives.

Due to the variance in stage duration, diversity indices were time corrected with the stage duration (Δt , MYr) as suggested by Ruta et al., (2011). This involved dividing all indices (measures of diversity) by Δt per stage to give a value of genera per million years for each stage to remove the potential bias of long stages yielding high numbers of species.

The total number of stereospondyl genera reported from each continent varied from three in Asia to 57 in Europe (Table 3.1 in results). The diversity (number of genera) for each geographic location was expressed as a percentage of total per stage in order to detect the differences in diversity patterns, and to avoid losing any signal in the noise of total numbers.

3.2.3 Fossil record correlations

To investigate whether the stereospondyl fossil record was robust enough to use in a diversity study, a small number of proxies were tested for correlation against diversity and against each other. Tetrapod bearing fossil formations (TBFF), completeness, stage duration and diversity (total genera), were all tested against each other for correlation, using Spearman's *rho* in R v 3.1.2 (R core team, 2016).

The uncorrected diversity count, TBFF, completeness and the stage duration were subjected to generalised differencing before correlation. Any test of correlation or regression assumes that the two variables are independent and time series data, such as we had here, might not be. Long term trends (for example, an increase in diversity) or a short term trends (e.g. the persistence of a genus from one stage to the next) breach these assumptions. Generalised differencing is when data are detrended then corrected for autocorrelation. This is done by differencing values in sequential stages, then correcting for the autocorrelation between successive stages (Benson and Butler, 2011). Generalised differencing was carried out in R v3.1.2 using Graeme Lloyd's 'functions_2.r' script (R core team, 2016; www.graemetlloyd.com).

As correlation exists between diversity and TBFF, Chi Squared goodness of fit was used to compare actual and predicted genus distributions and so identified times and locations of high coincidence. The TBFF distribution through time and total genus number were used to predict stereospondyl genus diversity, which was then tested against actual diversity. This method was not without its flaws as the total predicted number comes from the known stereospondyls but the true total number of stereospondyls will never be known. This method allowed the exploration of the data to a greater extent than simply recognising the correlation by examining the proportional distribution where the actual count of genus per location is less important.

3.2.4 Origination, extinction and persistence through time

Rates of origination and extinction are widely used metrics, which were used here to gain insight into the turnover of genera and their survival through mass extinctions. An origination was defined as the first known occurrence of a genus in the fossil record, whereas an extinction was the last stage in which it was known to occur. The total duration in the fossil record was recorded for each genus and the extinction and origination values were taken from this information, ensuring that the total number of extinctions matched the total number of originations. For each stage, these values were expressed as percentage of the total number of originations or extinctions in that stage.

The final element to consider was the persistence of genera across different stages. Taxa within a stage were assigned to one of two categories, those that are only known from a single stage ('single'), and those that persisted across one or more boundaries ('multiple'). The proportions of singles and multiples in each stage were examined across time. The

number of genera in a stage that had persisted from a previous stage was also examined across time.

Tests for association between origination and extinction events were not carried out because these metrics violate statistical assumptions: the confounding error of time series is that they are not independent from each other. The issue is further complicated by the inherent lack of independence between the two correlates, an extinction cannot happen without an origination, and we know that all of the genera went extinct at some point. The former issue could be adjusted using generalised differencing but to correct for the latter issue is a process that is only suitable for much larger data sets, the variance in smaller data sets would be diminished and as such provide a false impression of the data. In the interest of maintaining the integrity of the data, this information will only be used as a qualitative insight in to the distribution of stereospondyls in the fossil record.

3.3 Results

3.3.1 Distribution in the fossil record

The stereospondyl fossil record data began in the Moscovian (305.2 – 307 MYrA), with the first known stem stereospondyl, which was *Capetus palustris*, Steen 1938, from Germany. The last known stereospondyl, *Koolasuchus*, Warren, Rich, and Vickers-Rich 1997, was found in the Aptian of Australia (112-113 MYrA) following a 49.1 MYr gap in the fossil record. The distribution was global by the Traissic (Table 3.1). The time difference poses questions of why a stereospondyl would appear so long after the apparent extinction of the group, immediately demonstrating that there are absences in the fossil record. However all analyses were restricted to the end of the Toarcian due to the large gap before the next find (174.1 MYrA). A basic plot of the genera counts in stages (Figure 3.2, blue line) showed a slow and fluctuating increase, followed by a sharp increase in diversity at the start of the Triassic (grey line) when stereospondyl diversity peaked at 42 genera in the Induan (252.17-251.2 MYrA). There was a slight decrease in diversity in the Olenekian (251.2-247.2 MYrA). A gradual decrease followed, to a gap in the fossil record from the Hettangian (201.3-199.3 MYrA) to the end of the Pliensbachian (190.8-182.7).

When the values in each stage were divided by the duration of that stage, the diversity increase in the Induan was even more pronounced (Figure 3.2, red line). The fluctuations before and after the Permian-Triassic boundary (PTB) were lower and smoother. The

average diversity of genera per MYr was 2.94, but there was considerable variation with a standard deviation of 8.83 genera per MYr.

The stereospondyls occupied stages that range in duration from 18.5 Myr (Norian) to 0.97 Myr (Induan). Mean stage duration was 6.21 Myr ($SD \pm 3.70$). The diversity ranged from 0 to 42 genera per time bin and was far from evenly distributed. The two stages of the Early Triassic, the Induan and Olenekian, were quite short in duration (0.9 and 4 MYr respectively), but had the highest numbers of genera, (42 and 39 genera). The longest stage was the Norian, in the Late Triassic, 18.5 MYr, with 9 genera. There was no significant correlation between the duration of a stage, and the number of genera present ($\rho = -0.277$, $DF = 21$, $p = 0.238$; Figure 3.3). From this it might be concluded that changes in stage duration were not responsible for changes in diversity.

Overall mean quality (ranked from 1 to 4) for all stages was 2.36 ($SD \pm 0.71$). Mean completeness per stage ranged from 4, represented by one genus, *Sclerocephalus* (Goldfuss, 1847) in the Gzhelian, to 1.4, represented by five genera in the Changhsingian. There was no correlation between completeness and the number of genera in a stage ($\rho = -0.321$, $DF = 21$, $p = 0.194$; Figure 3.4). These results showed that the high diversity was not a result of a high number of species being described from poor material.

Overall, the longer stages yielded more complete specimens, but a closer look at Figure 3.5 showed considerable variation for both stage duration and mean completeness. The Asselian had quite complete specimens, with a mean of 3.75 from 4 genera. There was a significant positive correlation (illustrated by the regression fit line in figure 3.5) between stage duration and the mean completeness of taxa in that stage, though the model does not explain all of the variance in the data ($\rho = 0.508$, $DF = 21$, $p = 0.031$, Figure 3.5).

A correlation existed between the number of genera present and the TBFF (Table 3.3 appendix I). Figure 3.6 shows that there is considerable resemblance between the peaks and troughs of genera diversity and the TBFF. When the data are split into (modern) continents, these correlations persisted in most cases with the exceptions of South America and Asia, both of which have very low numbers of genera (Table 3.2). Most of the ρ values were not high, indicating that though there is correlation, it is not necessarily strong so further investigation was carried out to identify the areas where stereospondyl diversity differed from the TBFF.

Table 3.1. Total number of stereospondyl genera described from different continents over time

Age	Sum genera	Europe	India	N America	S America	Africa	Australia	Greenland	Asia
Bashkirian	0	0	0	0	0	0	0	0	0
Moscovian	1	1	0	0	0	0	0	0	0
Kasimovian	0	0	0	0	0	0	0	0	0
Gzhelian	1	1	0	0	0	0	0	0	0
Asselian	4	4	0	0	0	0	0	0	0
Sakmarian	3	1	2	0	0	0	0	0	0
Artinskian	2	0	0	1	1	0	0	0	0
Kungarian	2	2	0	0	0	0	0	0	0
Roadian	7	6	0	0	1	0	0	0	0
Wordian	6	2	0	0	1	3	0	0	0
Capitanian	4	0	0	0	1	3	0	0	0
Wuchiapingian	5	0	0	0	0	4	1	0	0
Changhsingian	5	1	1	0	1	2	0	0	0
Induan	42	7	6	0	2	12	12	3	0
Olenekian	39	16	0	3	1	10	2	5	2
Anisian	16	6	0	3	0	6	0	0	1
Ladinian	9	2	7	0	0	0	0	0	0
Carnian	14	4	1	1	1	3	0	0	0
Norian	9	3	2	3	1	0	0	0	0
Rhaetian	2	1	0	1	0	0	0	0	0
Hettangian	0	0	0	0	0	0	0	0	0
Sinemurian	0	0	0	0	0	0	0	0	0
Pliensbachian	0	0	0	0	0	0	0	0	0
Toarcian	1	0	0	0	0	0	1	0	0
Sum	172	57	19	12	10	43	16	8	3

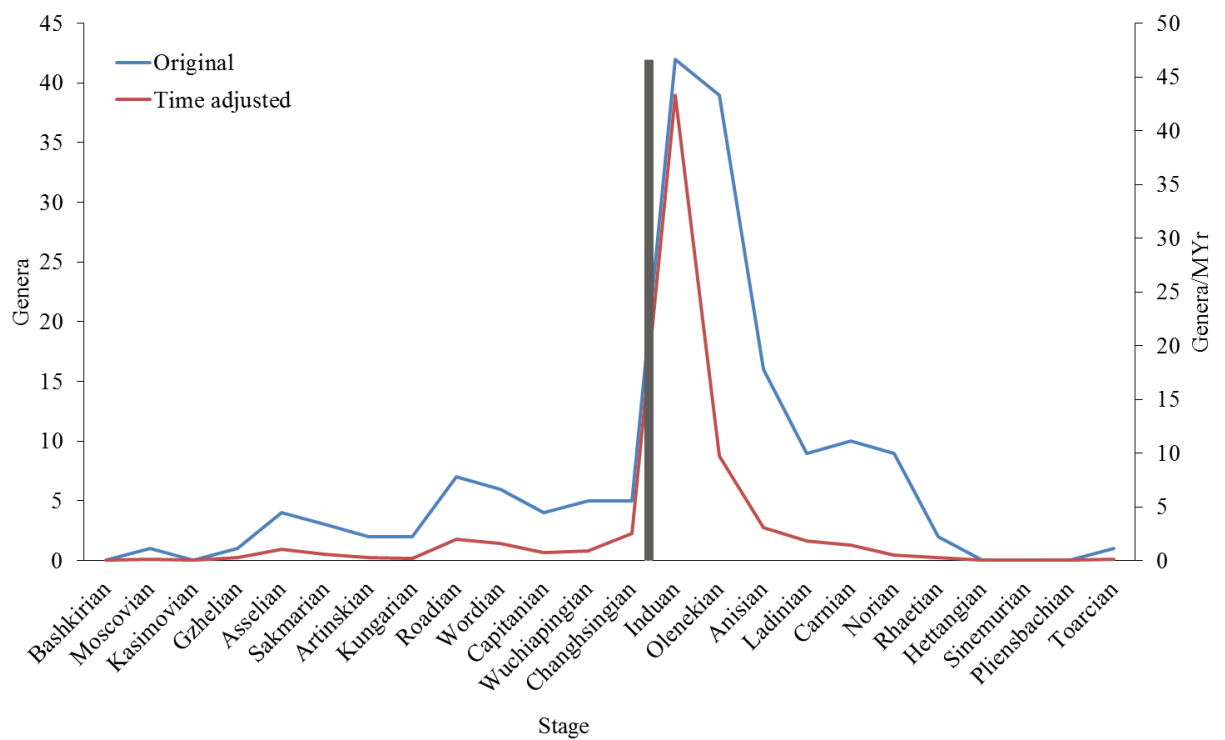


Figure 3.2 Diversity shown by number of stereospondyl genera over time with uncorrected (blue) and time corrected (red) distributions. The Permian-Triassic boundary is marked by a grey line.

TBFF numbers were used in conjunction with stereospondyl numbers to create an expected number of stereospondyl genera for each stage. The resulting predicted values were tested against the actual observations and chi squared goodness of fit test demonstrated that the predicted and actual values differed significantly (Table 3.2, Figure 3.7). Closer examination of the values (Figure 3.7) revealed that the stereospondyl genera numbers were substantially higher than predicted from TBFF in the Early Triassic. Conversely, the Late Triassic onward shows that stereospondyl diversity is lower than expected, which is also the case in the Carboniferous and Late Permian. It could be cautiously suggested that the Early Triassic peak in stereospondyl might signal a true peak in diversity, though the TBFF is only one of many proxies for fossil record completeness.

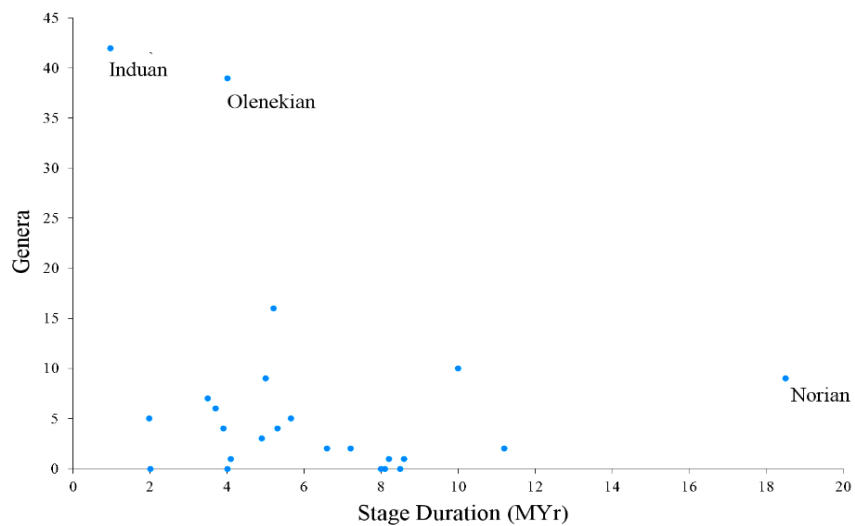


Figure 3.3 Duration of stage and stereospondyl diversity, reflected by number of genera present. There is no correlation between the two variables. Stages with unusual observations have been labelled.

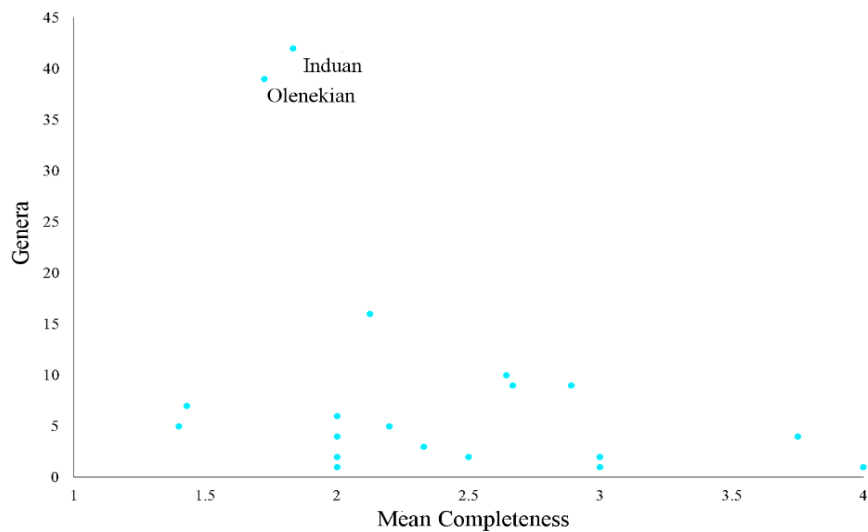


Figure 3.4 Mean completeness per stage and diversity of stereospondyl genera. Stages of unusually high diversity have been labelled.

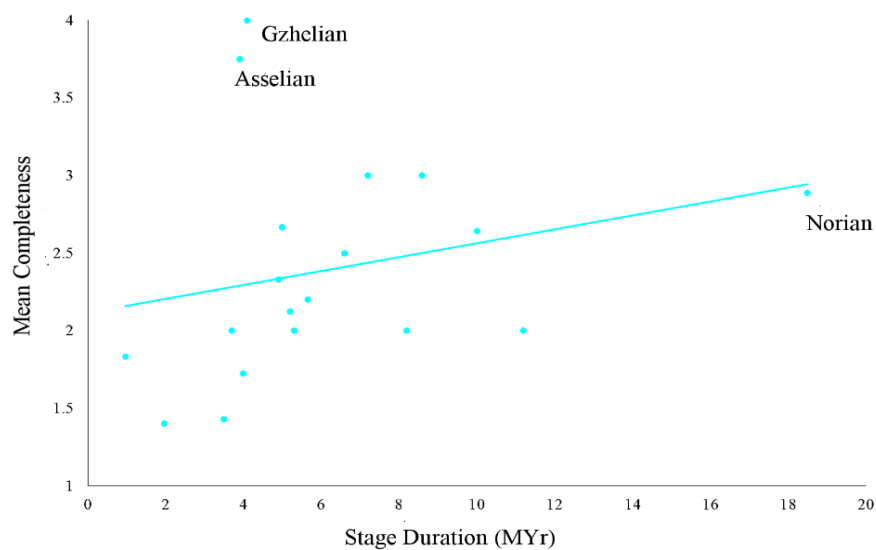


Figure 3.5 Mean completeness per stage and duration of time bins (MYr). Stages of unusually high diversity have been labelled

Table 3.2 Correlation and chi squared results of global and continental diversity

Area	Rho	P	Chi Square	P
All	0.502	0.019	236.021	<0.0001
Europe	0.542	0.008	95.301	<0.0001
Africa	0.495	0.017	52.838	0.0001
N America	0.487	0.019	37.662	0.014
S America	0.392	0.065	22.55	0.368
Australia	0.819	<0.0001	18.417	0.622
Asia	0.244	0.261	9.071	0.989
Greenland	0.737	<0.0001	9.000	0.989
India	0.593	0.002	43.242	0.003

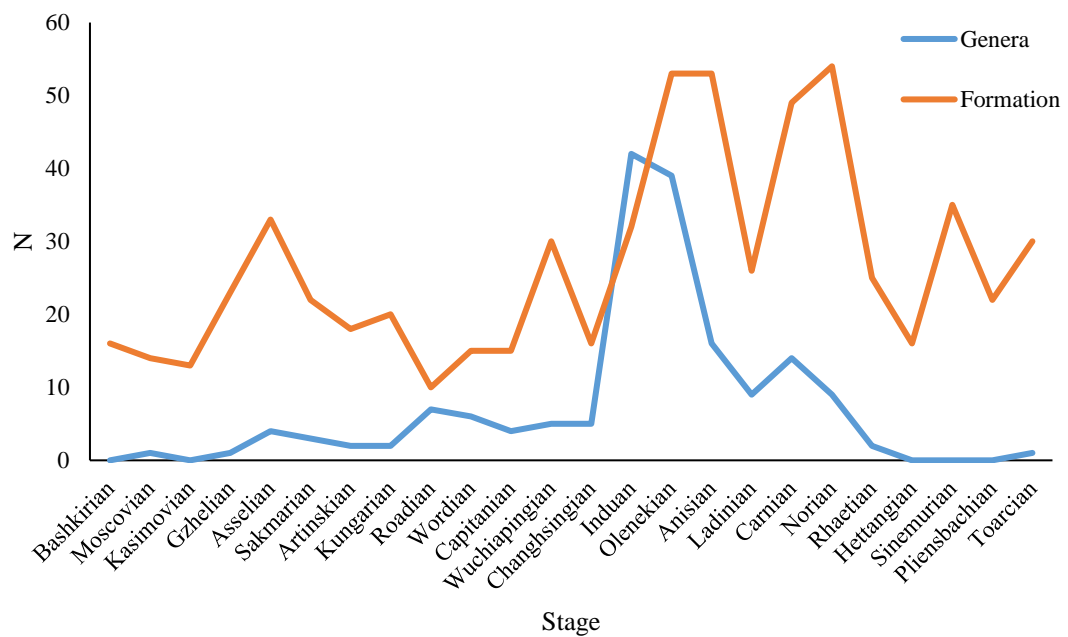


Figure 3.6 Stereospondyl diversity over time, represented by the number of genera present, is shown in blue and number of tetrapod bearing fossiliferous formations over time is shown in red. Spearman's rank correlation test shows a significant correlation between generalised differenced stereospondyl diversity and the number of tetrapod bearing rock formations ($p=0.019$, $\rho=0.502$).

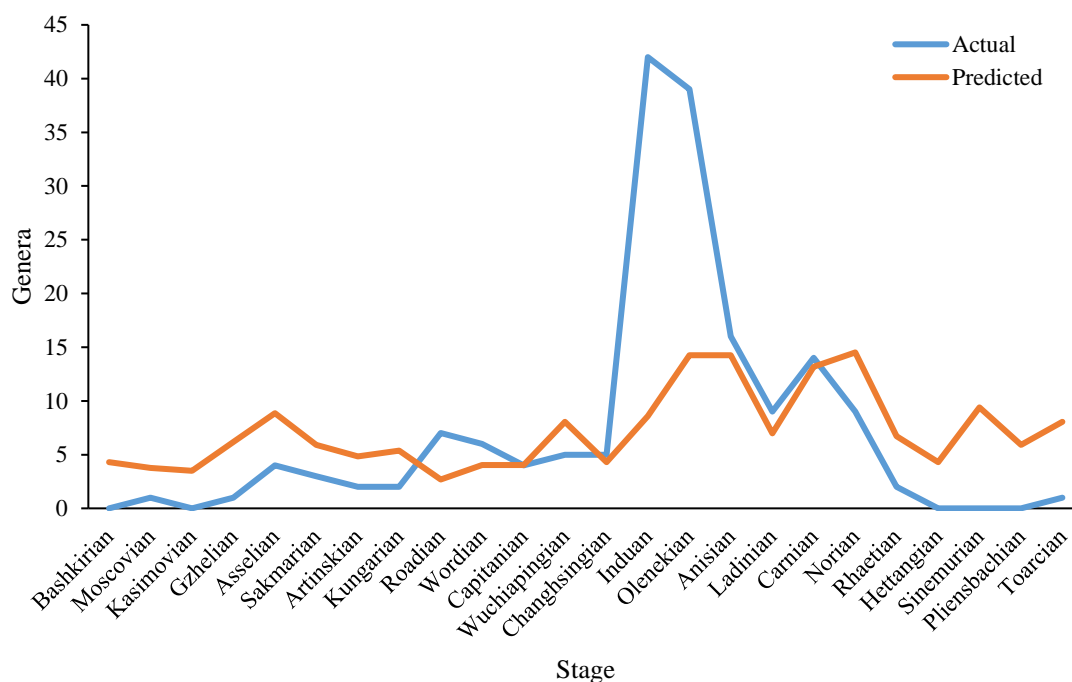


Figure 3.7 Chi squared goodness of fit showed a significant deviation of actual stereospondyl diversity from expected diversity based on TBFF. Actual observations are shown in blue, predicted observations are shown in red.

As previously mentioned, stereospondyl distribution was global but it was not evenly distributed over continents (see table 3.1). Chi squared goodness of fit demonstrated that, similarly to the global results, several continental level stereospondyl distributions differed significantly from those predicted from TBFF distributions. The exceptions to this were the less speciose South America, Australia, Asia and Greenland (Table 3.2, Figure 3.8). All continents showed a diversity peak at the Early Triassic, in India this peak almost identically matched the TBFF prediction peak. Greenland's chi square result is driven by the two TBFF prediction peaks and the fact that all stereospondyl finds in Greenland occur within the first TBFF prediction peak. Asia showed no difference between TBFF prediction and stereospondyl distribution but this is likely driven by the very low numbers of known stereospondyls ($n = 3$) as Asia has TBFF well through the Triassic and Jurassic (Benton et al., 2013). Figure 3.8 clearly demonstrates that South America's and India's stereospondyl diversity can be predicted from their TBFF numbers, suggesting that these continents may have been host to many more species of stereospondyls than we currently know about. The Australian fossil record is notoriously sparse due to the nature of the current and palaeo climates. Hot and dry climates are not

conducive to fossil preservation. The presence of stereospondyls well in to the Cretaceous demonstrates that there are tens of millions of years of stereospondyls unaccounted for.

Stereospondyls were largely absent from North America until the Triassic, despite the presence of other early tetrapods until the Middle Permian, notably including the well-studied non-stereospondyl temnospondyl, *Eryops*. The tetrapod fossil record is not well preserved in the Late Permian and Permian Triassic boundary of North America, so the absence of stereospondyls here ought to be attributed to preservation bias, though it could equally be the result of large parts of North America being under the ocean at this point.

Europe was host to the highest numbers of stereospondyl genera ($n = 59$, Table 3.1) and the highest number of TBFF ($N = 275$, appendix I, Benton et al., 2013). The early history of stereospondyls in the fossil record of Europe appears to have been driven by TBFF, the peaks and troughs of known genera up to the Middle Permian are likely not true changes in stereospondyl diversity, but a bias of the fossil record (Figure 3.8). However after the mid Permian there is substantial deviation from the predicted pattern, despite low numbers of TBFF in the Induan, stereospondyl diversity was rapidly increasing, it exceeds predicted values through the Early Triassic. However, as other tetrapods were continually found from Europe through the remainder of the Triassic and Jurassic, stereospondyls, with the exception of a brief resurgence in the Carnian, were much lower than predicted. Stereospondyls seem to have been absent when other tetrapods were present.

TBFF were absent from the Carboniferous of Africa, and stereospondyl diversity in Africa was lower than predicted levels in the Permian, (Figure 3.8). Stereospondyl diversity was exceptionally high throughout the early and Middle Triassic, until the Ladinian. As in Europe, there was a brief resurgence in the fossil record in the Carnian, and stereospondyls were absent from the fossil record from this point forward though other aquatic and terrestrial tetrapods were present in Africa during the Jurassic.

As there were several points in the fossil record where stereospondyls were absent but other tetrapods have been found (as evidenced by the presence of TBFF) it becomes pertinent to consider whether these other tetrapods were non-stereospondyl amphibians, likely to be direct competitors with stereospondyls, or if they are amniotes, many of which may exhibit different life history characteristics. We can see from Figure 3.9 that non-stereospondyl amphibians dominated the fossil record in the Carboniferous when most TBFF have been found in Europe and North America. As amphibians declined through the Permian, amniotes continued to increase, as the number of TBFF in Africa

increased. Although the total number of amniotes remained higher than amphibians including stereospondyls, it is clear that stereospondyls fared much better than amniotes following the end-Permian mass extinction (Figure 3.9). Amniotes appeared to recover for the remainder of the Triassic, which is where stereospondyls generally start being present in lower than predicted numbers in the fossil record (Figures 3.7 and 3.8). Non-stereospondyl amphibians were poorly represented from the Middle Triassic onwards.

3.3.2 Originations, extinctions and persistence

Three other measures of diversity were employed to assess stereospondyl diversity in the fossil record – rates of origination, rates of extinction, and the persistence of genera through stages. To mitigate the effects of the Early Triassic dominance in diversity origination and extinction rates per stage were converted to percentages of total originations and extinctions. Origination and extinctions were examined as both uncorrected and time-adjusted values (percentage originations/MYr; percentage extinctions/MYr; Figure 3.10).

The Carboniferous and Permian had low and fluctuating distributions of stereospondyl originations and extinctions, their uncorrected curves did not follow each other exactly, there was a small peak in originations in the Roadian. Looking at the Permian (the Roadian to the Capitanian), we can see that the small origination peak was followed by a sharp fall in originations, which was accompanied by a lower but longer extinction occurrence (Figure 3.8). The proportions of extinctions remained higher than originations until the end of the Permian (end Changhsingian, 252.17 MYrA), supporting the entire taxic turnover at the end of the Permian.

The Early Triassic again showed substantial change with a third of all stereospondyl originations occurring during the Induan (Figure 3.8). The uncorrected data showed several stages that had higher proportions of extinctions, most notably the Olenekian, which had 24 originations, and 35 extinctions (Figure 3.8). Indeed, only four stereospondyl genera survived from the Early Triassic into the Middle Triassic though the Middle Triassic has fewer TBFF than the Middle and Late Triassic so there was potential for fossil record bias.

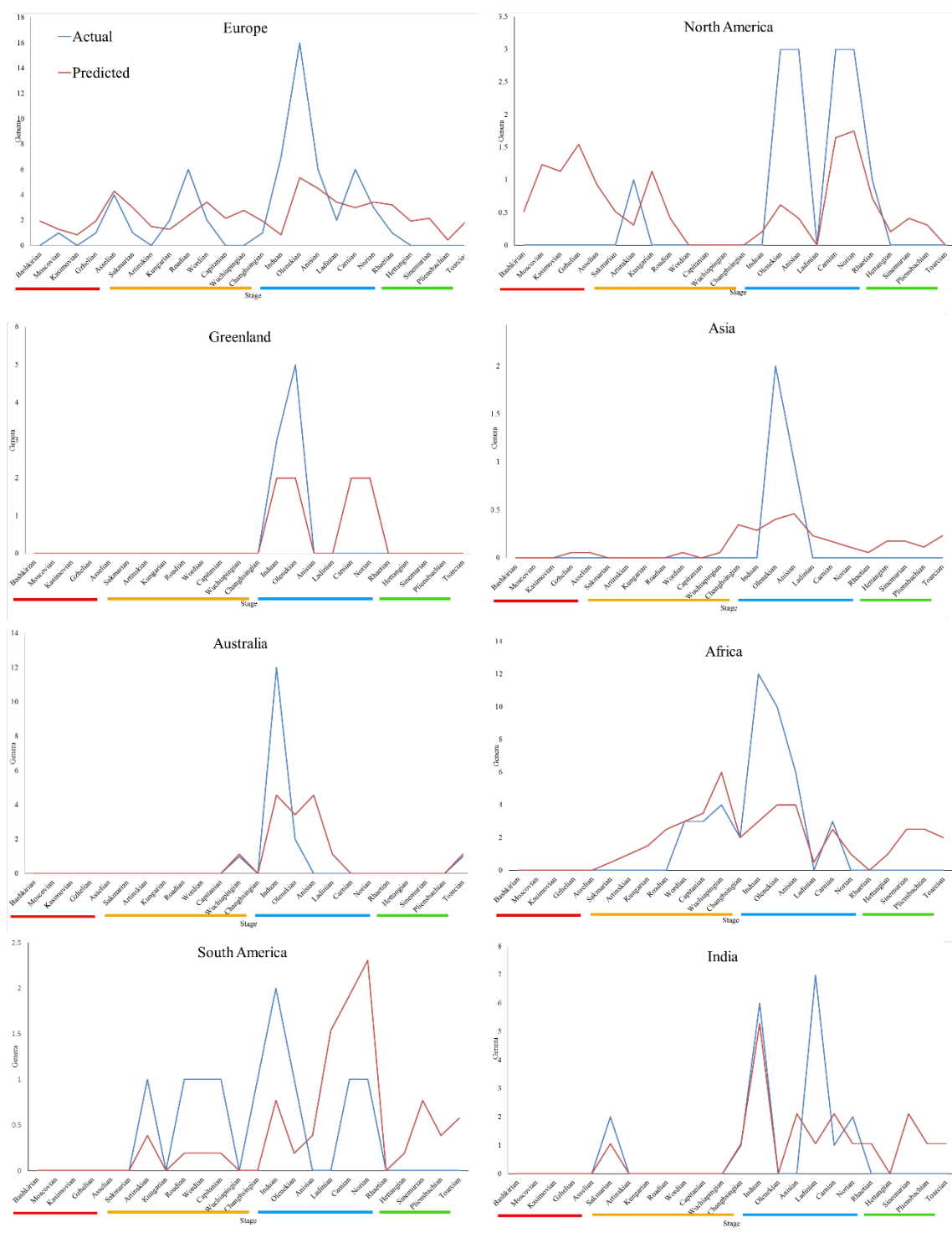


Figure 3.8 Stereospondyl diversity across continent and stereospondyl predicted diversity from TBB. Longer time periods are identified by coloured lines, red = Carboniferous, Orange = Permian, Blue = Triassic, Green = Jurassic.

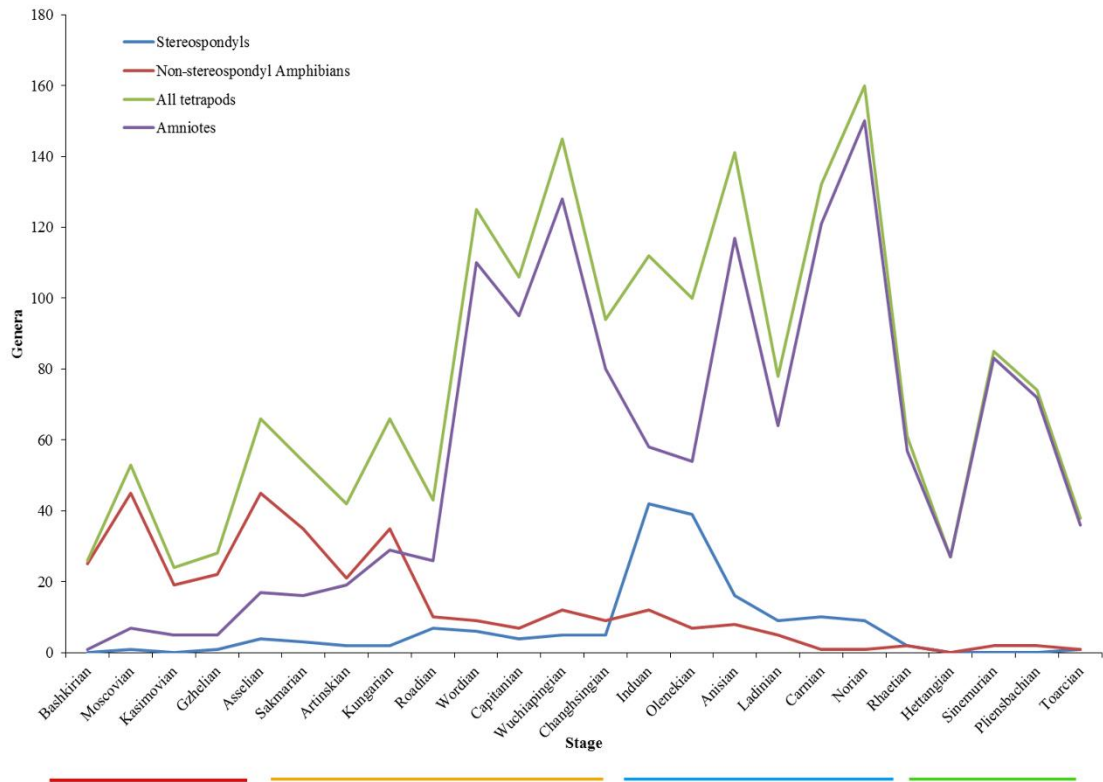


Figure 3.9 Number of genera of amniotes and amphibians across time. Longer time periods are identified by coloured lines, red = Carboniferous, Orange = Permian, Blue = Triassic, Green = Jurassic.

There appeared to be an overall reduction in rates of both originations and extinctions in the Anisian and Ladinian, the two stages of the Middle Triassic, possibly attributable to a generally poorly preserved period in geological time. The Late Triassic saw more TBFF globally (appendix I) but overall fewer stereospondyls. The Carnian had one final peak in the number of originations, but the extinctions were higher until an absence of stereospondyls from the fossil record. The Late Triassic had fewer overall taxa than the early and Middle Triassic, and fewer originations, particularly when time calibrated (Figure 3.11).

Time-correction dampened many of the fluctuations in the originations and extinctions, particularly in the Middle and Late Triassic (Anisian onwards). The per million year rates of extinction and origination matched each other, almost perfectly, with the exception of the high proportion of “extinction” in the Olenekian (Figure 3.11). It can be concluded that the Early Triassic was an eventful time in the fossil record for originations of stereospondyls, which accounted for most amphibian finds in this period.

There was a difference in the persistence of genera across stages (Figure 3.11). Only one stereospondyl genus, *Arachana*, a single skull find from the Buena Vista formation in Uruguay, appeared to have survived the end Permian mass extinction. Describing this taxon, Pinero et al., (2012) put the formation at the Permian Triassic Boundary, though it was allocated as Induan in the early Tetrapod database of Benton et al., (2013). To be conservative, I followed Pinero and colleagues' wider range rather than attempting to justify a more precise time period. Very few genera in the Early Triassic were present in the Middle Triassic, shown in Figure 3.11 by the drop in the persistence curve, which is consistent with the drop in TBFF in the Middle Triassic. The Middle Triassic had more genera that persisted in to the early stages of the Late Triassic, shown by the peak in the Norian.

Most genera were present in only a single stage (97 of 130 genera). Twenty-six genera persisted over two stages whereas five genera persisted over three stages. *Mastodonsaurus* and *Cyclotosaurus* persisted over four stages of the Middle and Late Triassic (periods of 24 and 40 MYr respectively).

The proportion of single time bin genera is higher than multiple time bin genera in almost all stages (Figure 3.12). The Gzhelian had only one genus, and was the origin of *Sclerocephalus*, which was present in the fossil record until the end of the Sakmarian. The four genera in the Capitanian were all multiples, one originating in the previous stage (*Australerpeton*) and the other three surviving into the Wuchiapingian.

In the Induan 62% of the taxa were present only in that stage (Figure 3.1) despite the Olenekian having large numbers of TBFF. Given that the Induan was the shortest stage assessed here (0.9 MYr), this suggests that there were a lot of short lived taxa at the start of the Triassic. Of the 42 genera in the Induan, only 15 persisted into the Olenekian.

The Anisian, the start of the Middle Triassic, had a high proportion of singles (69%), and only two genera, *Mastodonsaurus* and *Eryosuchus*, survived in to the next stage, through this could be a result of the previously mentioned poorly preserved era. The proportions of multiples increased slightly in the Late Triassic (Carnian onwards) when numbers of stereospondyls generally fell below the predicted levels. Multiple stage taxa accounted for 50, 67 and 50% of the genera present in the three Late Triassic stages (Figure 3.10). Most of the genera that are present in the Norian and Rhaetian originated in the Carnian.

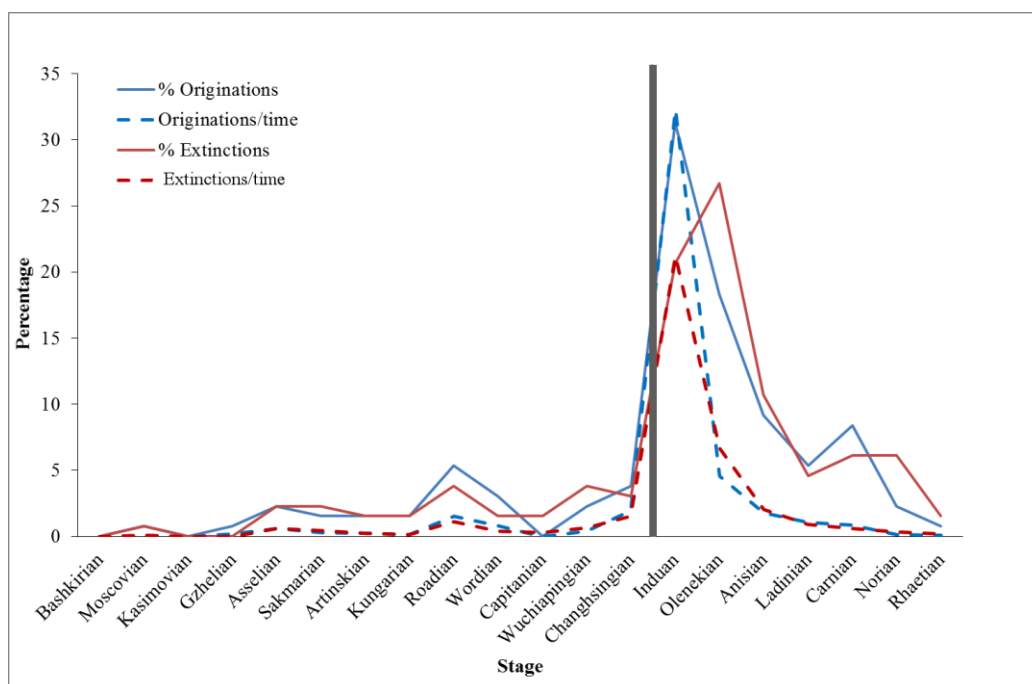


Figure 3.10 Originations and extinction rates of stereospondyls distributed across time bins expressed as percentages of all originations and extinctions respectively. Uncorrected percentages are shown with solid lines and time corrected have dashed lines. The Permian Triassic boundary is indicated by a grey line.

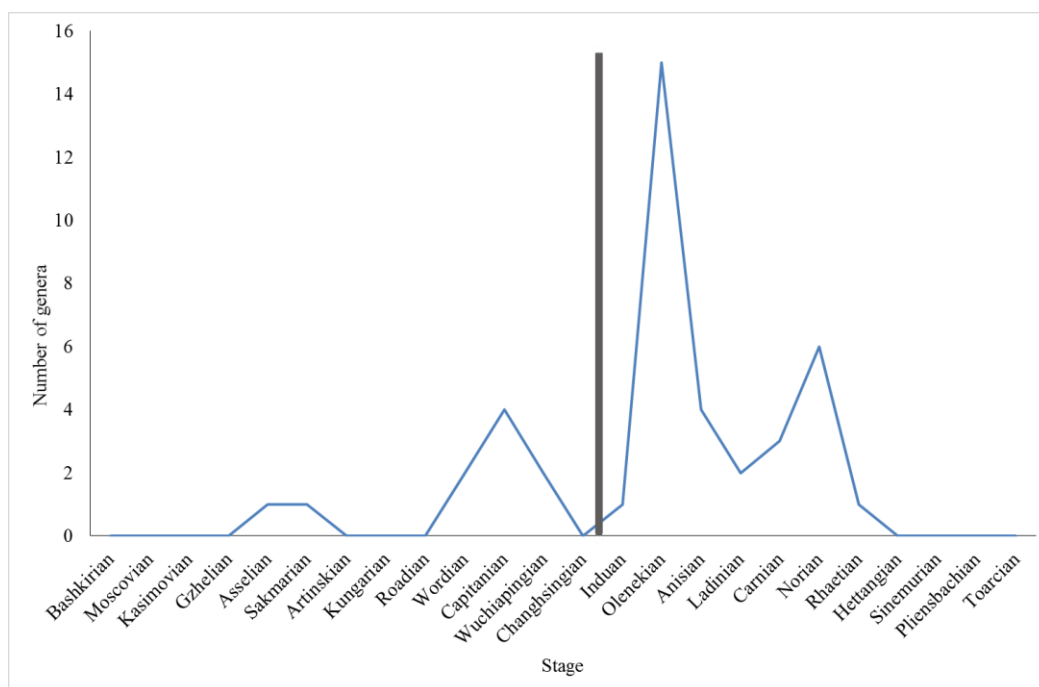


Figure 3.11 Number of genera persisting from the previous stage, the Permian-Triassic boundary is shown in grey

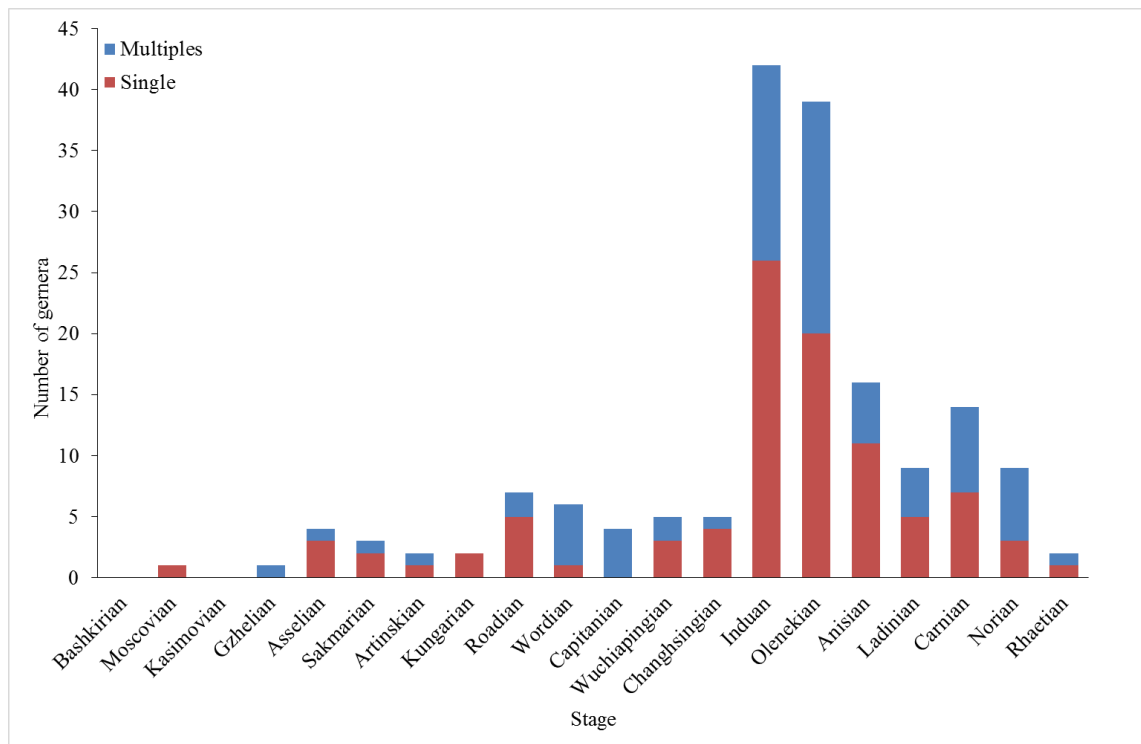


Figure 3.12 The proportion of single and multiple stereospondyl genera found in the various time stages.

3.3.4 Taxonomic distribution of stereospondyls

In this analysis stereospondyls are divided in eight taxonomic groups including stem stereospondyls (Schoch and Milner 2000). These were not equally distributed over time and places. Stem stereospondyls appeared to be restricted to Europe, though only Europe and North America had TBFF in the Carboniferous. By the Late Permian stereospondyls had diversified to four taxonomic groups in five continents, but they remained absent from North America until the Early Triassic despite North America being host to many other early amphibians. Stereospondyl diversity far exceeded predicted diversity in the Early Triassic, which is when the two most speciose taxonomic groups appeared to originate, the Capitosauroida and Trematosauroida. There were many gaps in the Middle Triassic, as previously discussed, but the Plagiosauroida make their first appearance. The better preserved Late Triassic still hosted lower than expected numbers of stereospondyls as many of the taxonomic groups failed to reappear in the fossil record. Australia was host to the post Triassic remnants of the stereospondyls with the Brachyopoidea, though there are substantial amounts of missing fossil material from Australia.

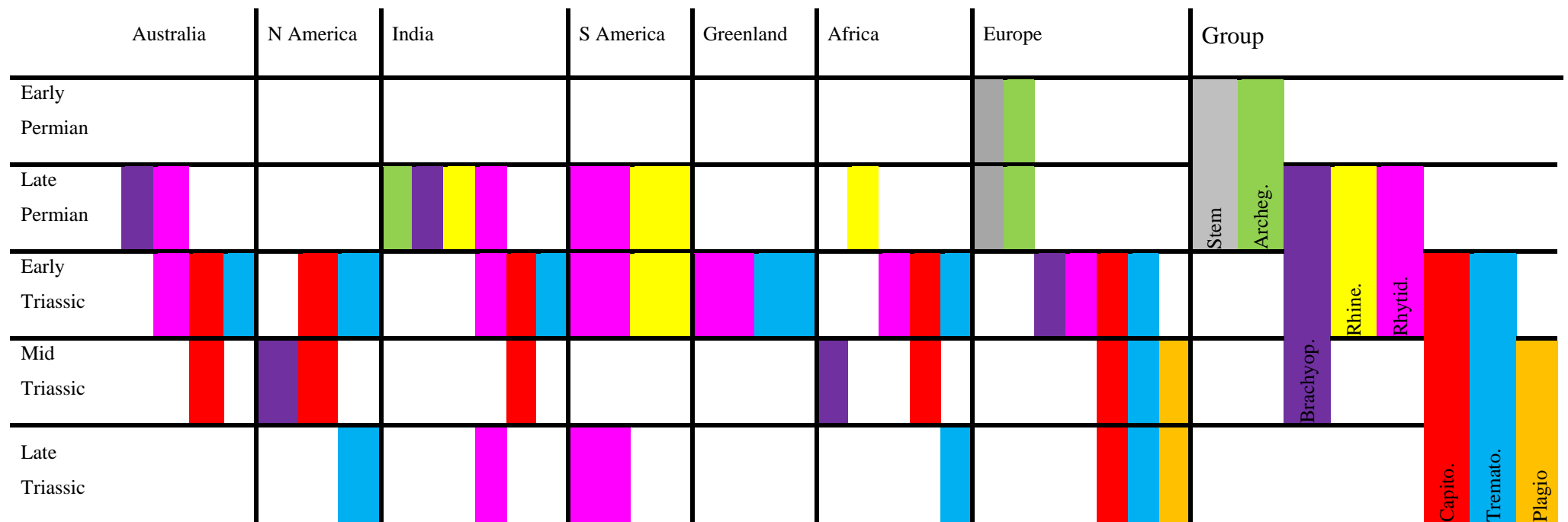


Figure 3.13 Taxonomic distribution of stereospondyls over time and locations.

3.4. Discussion

3.4.1 Distribution in the fossil record

Origin of stereospondyls

The first stem stereospondyl appeared just before a diversification event in the Carboniferous. *Capetus palustris* is described from the Moscovian of Germany, the stage that precedes the rainforest collapse of the Kasimovian (Sahney et al., 2010). As ferns dominated the plant fossil record, tetrapod diversification increased in Laurasia (Sahney et al., 2010).

The Permian climate is not as well understood as the Triassic, but the presence of the supercontinent Pangea meant that the inner areas (modern day Africa) were dryer than the outer edges, which included modern day Eurasia and western parts of North America. As the amniote synapsids appeared to have dominated the land fossil records (Modesto et al., 2011) the Permian became home to a steadily increasing number of stereospondyls. The earlier stages and middle stages of the stereospondyl Permian record were dominated by European genera, particularly the Archegosauridae, with an absence of stereospondyls in North America. Several non-stereospondyl amphibians such as *Eryops* and several species of Dvinosauria have been found from several North American locales of the Permian (Yates and Warren 2000), but the tetrapod fossil record of North America is better populated with sister amniotes such as *Diadectes* and the reptile-like *Seymouria*. The North American climate was mostly arid in the Permian, with the exceptions of the coastal areas, much better suited to terrestrial species. With the exception of the Dvinosauria, most of the North American genera were fully terrestrial (Modesto et al., 2011). Many of them reached much larger sizes than the European stereospondyls.

Much of the Southern areas of Pangea were under ice caps in the Early Permian and the remainder was cold and arid. Stereospondyl genera numbers increased in southern continents toward the end of the Permian by which time the earliest known members of the Brachyopoidea (India and Australia), Rhinesuchidae (Africa and India) and Rhytidosteoidea (India) were present. Superficially, it would appear that as the ice caps covering southern Gondwana receded, stereospondyls colonised the new habitat (Benton and Newell, 2014). However, stereospondyl genera numbers are tightly correlated with the numbers of TBFF in the immediate stages before the PTB. The Permian environment does appear to have suited amniotes more than amphibians, as the former rely less on

water than amphibians, which need water for at least part of their life cycle (Frobisch et al., 2010).

The end-Permian extinction has been described as the largest of the Phanerozoic, and primarily physiological in nature (Raup and Seposki, 1982, Clapham and Payne, 2011). This conclusion is on the basis of marine invertebrates, as tetrapods from this period are lesser known. There is evidence to suggest the end Permian events, which stereospondyls survived, were unfavourable to those who had poorly buffered respiratory physiology and so were highly susceptible to change (Clapham and Payne, 2011) such as the rising ocean carbon dioxide and temperature. Few stereospondyls have been described as marine, but these oceanic changes clearly had an extinction effect on aquatic and land ecosystems (Lucas and Tanner, 2015). Despite this catastrophic event, stereospondyls do not appear to have gone through an ecological bottleneck at the PTB, which many of the non-amphibian tetrapods did. The greatest peak in stereospondyl genera diversity came immediately after the PTB, when most life on earth was still recovering.

Early Triassic stereospondyls

Stereospondyls may have been able to travel from river mouth to river mouth to feed and mate, rather than having to travel across land. An increase in the drainage and lacustrine environments in the Early Triassic might reduce habitat fragmentation for fluvial species that could tolerate brackish and marine waters. In addition on land there was little vegetation cover to protect them from the acid rain (Benton and Newell, 2014). It is possible that the scaled stereospondyls were less susceptible to desiccation than modern amphibians with their porous skin. The increased mobility from increased aquatic environments combined with some protection from dermal scales might increase their ability to disperse, thus potentially reducing inter and intra species competition.

The Karoo of South Africa and the Russian basins were both now arid environments where they had formerly been humid, yet were home to many stereospondyl species in the Early Triassic. It would appear that stereospondyls were able to not just survive, but to thrive in these environments. Stereospondyl diversity exceeded predicted diversity in almost all continents in the Early Triassic, so it is possible we observed a genuine peak in diversity.

The Karoo Basin of South Africa is a well-studied and non-marine basin. It is a productive basin that has yielded many stereospondyls (Damiani, 2004). In the years prior to the PTB, it showed evidence of increasing seasonality, progressing to monsoon activity,

eventually becoming arid in the Early Triassic (Smith and Botha-Brink, 2014). These changes altered the vegetation, with the effects of forest loss moving up the ecosystem (Smith and Botha-Brink, 2014). Several taxonomic groups of stereospondyls are known from the Karoo Basin, including the most speciose Capitosauroida and Trematosauroida (Schoch and Milner 2000, Benton et al., 2013), alongside non-stereospondyl temnospondyls, Dvinosauria and Dissorophoida (Benton et al., 2013, Warren 1998, Damiani 2004). The Archegosauridae did not survive into the Triassic and although the Rhinesuchidae have been reported from the Early Triassic of South America, this species was *Arachana nigra*, was only reported in the Early Triassic of Uruguay because the formation it yields is described as both Late Permian and Early Triassic. The Rhinesuchidae are also poorly resolved taxonomically, so it is possible that *Arachana nigra* is not a true Rhinesuchidae and has been incorrectly assigned to the group when all other South American taxa are assigned to the Rhytidosteoidea.

The Karoo was likely colonised by stereospondyls that were better adapted to survive an arid climate, possibly those with a smaller body size. Smaller body sizes are better able to withstand higher temperatures, particularly amongst ectothermic animals (Kingsolver and Huey, 2008). It has been suggested that the South African species were likely able to survive on a diet of fishes or small aquatic invertebrates that occurred in sufficient quantities to support them (Jeannot et al., 2006). These aquatic feeding strategies would mean that they would be less affected by the loss of vegetation, than the land animals, a suggestion that warrants further investigation with morphological interpretations.

Lydekkerina huxleyi is one of these well-known stereospondyls from the Early Triassic of South Africa. It features in many phylogeny studies of stereospondyls and has many specimens attributed to the species. It was comparatively small and, as suggested by bone histology, employed a maturing early and dying young life history (Canoville and Chinsamy, 2015). It comes from the Induan stage which followed the largest known mass extinction (Raup and Seposki, 1982), and *L. huxleyi*'s life history strategy, coupled with a terrestrial mode of living, seemed to aid the success of this particularly abundant species. The small size may have helped *L. huxleyi* survive in the hot climates of the Early Triassic.

L. huxleyi was typical of many other stereospondyl species of the Induan in one way, it is only known from that one stage. The high origination in the Early Triassic was matched with high extinction despite the Olenkian having sufficient TBFF to still host stereospondyls. These numerous genera were short lived in the fossil record. Different

geographic locations have shown variance in the rates of origination across the PTB, in tetrapods as a whole, higher rates have been observed in Russia than South Africa (Shishkin et al., 2006; Benton and Newell, 2014). The opposite is true in stereospondyls, though stereospondyls were increasing as other non-stereospondyl amphibians and amniotes were taking their time to recover after the PTB.

At this stage we know that stereospondyls showed a large increase in species diversity in the Early Triassic, higher than predicted from TBFF and higher than other tetrapods, and that turnover was high. There is the sceptical, and unlikely, suggestion is that taxic turnover is an independent response to the abiotic factors (Alroy, 1996). More likely it is the result of mass extinction and ecosystem remodelling provides huge opportunity to the surviving clade. New or previously unexplored niches allow expansion with less competition and provide ideal opportunities for rapid diversification (Ruta et al., 2013). It would appear that stereospondyls took advantage of the absence of competition or predation, and rapidly diversified in many species.

Because species occur when reproductive isolation happens, the rate at which new species appear is linked to the physical barriers that cause reproductive isolation (Benton and Pearson, 2001). Physical distances can create barriers so if mobility is high species can occur when individuals move to new areas. Rivers are linked to larger water bodies such as seas and lakes, so something that can survive with brackish water can move between the mouths of rivers. This could have enabled stereospondyls to disperse into new locations more easily. The stereospondyls had mobility created by large river deltas, and a tolerance for brackish waters (Schoch and Milner, 2000). They had reduced competition due to the absence of other tetrapods, particularly other amphibians. They may have had physiological adaptations to the climates, as well as physical ones. This resulted in a rapid expansion and global distribution of stereospondyls in the Early Triassic.

Individual physiology has been cited as a survivability factor in mass extinction involving changes in oxygen and carbon dioxide composition (Benton and Newell, 2014). Some marine invertebrates reduced in size in response to the Permian Triassic event (Metcalf et al., 2013), smaller bodies are better adapted to high temperatures in exothermic animals (Kingsolver and Huey, 2008; Gardner et al., 2011). It is quite likely then that the stereospondyls that were so successful in the high carbon dioxide environment of the Early Triassic may have had adaptations to the harsh environments.

Middle Triassic stereospondyls

Stereospondyls had a largely northern distribution in the Middle Triassic but southern continents had very few TBFF so this distribution must be considered with caution. Stereospondyls have not been found in the fossil record of Greenland from the Middle Triassic onwards but there are no Middle Triassic TBFF in Greenland. There was greater separation between the Gondwana and Laurasia in the Middle Triassic as the Tethys sea spread between them, and the Gondwanan continents had few stereospondyls. Globally, amniotes fared better than amphibians as climates stabilised in the Middle Triassic, though forests were still lacking (Benton et al., 2013). Australia had no stereospondyls in the fossil record until the Jurassic. Given the overall poor quality of Gondwanan preservation, it seems unlikely that stereospondyls were truly absent, since Africa and South America also had none in the second stage of the Middle Triassic. The global temperatures cooled and humidity increased in the Middle Triassic (Preto et al., 2010) as a result of the mountain formations and smaller land masses. During this time stereospondyls may have had fewer originations, but those that originated, persisted in the fossil record for longer than their Early Triassic counterparts.

The Plagiosauroidae originated in the Middle Triassic of Europe and persisted into the Late Triassic, only a small number of species are presently known and they yield from the productive and well-studied Lettenkeuper formations of Germany. Most notable about this taxonomic group is that their morphology seemed to be substantially different from the other European stereospondyls. Whilst much of the diversity information from the Middle Triassic must be approached with caution, the origination of Plagiosauroidae seems certain. The restriction of the group to Europe should not be considered certain.

The Middle Triassic was host to more multiple time bin genera (proportionally), than the Early Triassic, which may be of some significance considering stereospondyls were likely underrepresented in this part of the fossil record due to low numbers of Middle Triassic formations. There is minimal information on the regional climates of the Middle Triassic, forests were still recovering, as coal seams are small and patchy (Retallack, 2013). It does seem that the three clades of the therapsids were able to persist through the first twenty million years of the Triassic, with the herbivorous and large dicynodonts and the smaller cynodonts (which evolved into mammaliaformes in the Late Triassic) surviving much longer (Modesto et al., 2011). Early archosaurs, the clade that eventually included dinosaurs, were increasing in number (Modesto et al., 2011).

Late Triassic stereospondyls

The length of the stages in the Late Triassic creates a false impression of species longevity. The imprecise nature of the three end Triassic stages is well established (Lucas et al., 2012), and so the duration of the stage must be considered here. It is possible that a single stage genus from a Late Triassic stage lived the same length as one from the very short Induan in the Early Triassic.

There was a decline of several families of stereospondyls through the Late Triassic, as overall diversity and originations decreased, stereospondyl diversity was continually lower than predicted values. Extinctions decreased in line with the decreased originations. The stereospondyls largely disappeared with the end-Triassic mass extinction, though we now know it was a series of smaller extinctions (Tanner et al., 2004, Lucas and Tanner, 2015). The end Triassic lacked global disruptions to ecosystems, with evidence supporting local niche disruptions (Lucas and Tanner, 2015). The stereospondyls seem to decline with these local extinctions, clearly lacking the adaptations required to survive.

Lucas and Tanner (2015) report that the plagiosaurs were the only family to go extinct at the TJB, rather than one of the earlier stages of the Late Triassic. Essentially this would mean that they were the only family with members present in the last stage of the Triassic. The data here show that *Apachesaurus* (Trematosauroidae) and *Cyclotosaurus*, (Capitosauroidae), went extinct at the final boundary of the Triassic, the former was only known from the Rhaetian. Nonetheless it is true that most stereospondyl genus level extinctions did take place before the TJB.

There was a bolide impact approximate 14 MYr prior to the TJB (Lucas and Tanner, 2015), placing the impact in the mid Norian. This created the CAMP basalt flooding that spanned the TJB (Cirilli et al., 2009). The knock-on effect was reduced production by phytoplankton, effecting the marine ecosystem. On land, the increase in atmospheric hydrogen disulphide could cause rapid cooling followed by long term temperature rises caused by carbon dioxide increases, resulting in increased biotic turnover (Lucas and Tanner, 2015). In the case of stereospondyls, these increased turnovers resulted in too few originations.

3.4.2 Taxonomic group distribution

Some tentative trends can be identified amongst stereospondyl taxonomic groups. Rhinesuchidae are an early occurring group that have only been found in the rarer southern formations of the Permian. At the same time the Archegosauridae are best known from Europe, alongside stem stereospondyls, though there is an isolated occurrence of an Archegosauridae from India (see Sengupta, 2003), suggesting that these stereospondyls may have a broader distribution than currently seen as there were fewer fossiliferous formations in the south in the Permian. Brachyopoidea was most common in Australia (Warren and Marsicano, 2000), though the Rhytidosteoidea had a considerable presence there as well. The metoposaurids (included in the Trematosauroida by Schoch and Milner, 2000) were the only large amphibians (skull greater than 25cm) in the Late Triassic of North America and India (Schoch, 2008). In the Late Triassic of Europe, ecosystems were shared by larger temnospondyls, the metoposaurs and the cyclotosaurids (Trematosauroida and Capitosauroida respectively) (Schoch, 2008).

Trematosauroida (including the metoposaurids) have been found in continental and marine deposits (see Schoch and Milner, 2000; Damiani, 2004; Fortuny et al., 2011) and are known from most northern deposits. The Capitosauroida were even more global, with representative from all continents throughout the Triassic. The taxonomic groups were well represented in India (Sengupta, 2003). Chigutisaur amphibians (within the Rhytidosteoidea) are known from India, Australia and South America, several early phylogenetic analyses placed the Indian species as a sister group to the others (see Marsicano, 1999). Marsicano suggested that this is evidence for the early isolation of India from Gondwana (Marsicano, 1999). *Parotosuchus*, within the Capitosauroida, is the most speciose genus of stereospondyls, known from Europe and South Africa (Damiani, 2001). This wide spread of taxonomic groups supports the notion that they lacked significant competition throughout the Early Triassic speciation event, but this should also be explored with respect to functional morphology, to provide niche occupation insight.

Only Brachyopoidea of Australia, have been found in formations dated after the Triassic. Unfortunately there are millions of years of fossils missing from the record as the arid environment of Australia both presently and historically is not conducive to fossil preservation. Jurassic formations that yield other tetrapods including amphibians are globally distributed with the exceptions of Greenland and Australia. Most notably the

Jurassic was home to the much larger amniotes, sauropods and theropods on land. Though these are very unlikely to have been direct competition for stereospondyls, a closer examination of the functional morphology of stereospondyls could provide insight into their extinction, was it caused by habitat disappearance or competition from the thriving amniotes.

3.4.3 Unusual observations in geological time

A large challenge with accurately dating temnospondyl occurrences is the confounding effect of how ages of strata are identified. Temnospondyls are frequently used to correlate Triassic facies (Fortuny et al., 2011). If the age of an outcrop or facie is designated according to the species that is in it, then the species is obviously going to be assigned to that age. If stereospondyl species are used to date Early Triassic outcrops, then there will clearly be a high number of stereospondyls described from the Early Triassic. Capitosauroides have been used in biostratigraphy zonation of Europe and South Africa (Damiani, 2001), confounding the diversity seen in the Triassic though amniotes are also used to date the *Cynognathus* and *Lystrosaurus* zones of the Karoo.

Assuming that the dating of the locales are correct, stereospondyls survived in to the Aptian. *Koolasuchus cleelandi*, Warren, Rich and Vickers-Rich 1997, was described from a mandible found in Australia. Also Australian, *Siderops kehli*, Warren and Hutchinson, 1983, was described from the Toarcian (Early Jurassic). Both are members of the Brachyopoidea. The dating of these two species is widely accepted amongst Australian vertebrate palaeontologists, they were both verified on the basis of pollen spores (personal communication Dr Scott Hocknull June 2016).

It would appear that Australia was a refuge for stereospondyls in the post Triassic (Warren and Marisicano, 2000). The older, *Siderops* is known from the Upper Evergreen Formation of Queensland, Australia (Warren and Hutchinson, 1983). They claim a Liassic age (the uppermost Early Jurassic), based on the presence of microfossils, with particular emphasis on *Classopollis classoides*, that they state are not known from any pre Jurassic formations. *C. classoides* is a pollen spore, known from over 240 collections globally (PalaeoDB, 2016). Most collections are from the Cretaceous, with ten from the Jurassic. There are two possibilities here, first, that *C. classoides* is accurately restricted to the Jurassic and Cretaceous, and the position of *Siderops* is accurate. Second, the date ranges of *C. classoides* are redundant, finds are dated as Jurassic due to the presence of

C. classoides itself, meaning the dating of *Siderops* is flawed. Given the global distribution of the pollen, it seems unlikely that all of the finds could be redundant, so we can tentatively accept the placement of *Siderops* in the Jurassic of Australia.

The second post Triassic, and much younger stereospondyl is *Koolasuchus*, placed in the Aptian, when described by Warren, Rich and Vickers-Rich, 1997. It was found in the Strzelecki Group of Victoria, Australia. The publication gives little information on the formation, which has been given a maximum age of Barremian (one stage older than Aptian), but little information is available on the methods used to date this stage (Australian Stratiagraphic Units Database, 2016).

3.4.4 Stereospondyl finds that are not attributable to species

Several stereospondyl finds have been reported in the literature that are not attributable to species, and so were not included in the analyses here, but they are still worth mentioning. A stereospondyl find from Turkey has been reported. It appears to be partial stereospondyl skull roof bone, based on the pustular pattern (Fortuny et al., 2015). The find itself is barely recognisable as a stereospondyl as it lacks diagnostic elements, it could be any temnospondyl. However irrespective of whether the find is a stereospondyl, it confirms the presence of amphibians in the Early Triassic of Turkey. It widens their Early Triassic range considerably, supporting a rapid turnover model in the Early Triassic (Fortuny et al., 2015). The most notable thing about a stereospondyl find in Turkey would be that Turkey was not part of the Supercontinent, Pangea, it was a small island in the ocean to the East of equatorial Pangea.

Stereospondyls have only recently been described from China (*Yuanasuchus laticeps*, Liu and Wang, 2005; *Yuanasuchus maopingchangensis* Lui, 2017). The presence of *Yuanasuchus* showed that the stereospondyls had reached China by the Middle Triassic, likely living in a river delta (Liu and Wang, 2005; Lui, 2016). A trematosaurid amphibian was reported from the Middle Triassic of China (Maisch et al., 2004). This dubious attribution is based on a single ilium, a conservative part of the temnospondyl anatomy. A partial mandible from the lower Triassic of Japan has been assigned to the Capitosauroida (Nakajima and Schoch, 2011). Scrap capitosaurid material has been described from Tasmania (Cosgriff and DeFauw, 1987). North-eastern North America has so far produced few stereospondyls that can be assigned to a species or genus, the material is largely fragmentary, and often ignored (Sues and Schoch, 2013). Though they

provide little functional information, these finds confirm a global distribution of stereospondyls, particularly in the Triassic even though the quality of the fossil record varies.

3.4.5 Proxies

Several proxies were assessed in an attempt to detect any redundancy between the quality of the stereospondyl fossil record, and stereospondyl diversity. The lack of correlation between species number, species completeness and stage duration indicates that this stereospondyl diversity is not an artefact of high numbers of species being attributed to poor material, or high diversity stemming from long stages. The correlation with TBFF is of no surprise as it is seen amongst tetrapods as a whole (Benton 2015). On closer inspection we can see that the correlation is driven by a lack of Middle Triassic formations in conjunction with generally poor Gondwanan records. As such we must treat diversity analyses of these times and locations with caution, though that is not to say we cannot interpret anything of stereospondyl diversity. Through the Early Triassic stereospondyls appear to have higher diversity than predicted by the number of TBFF, suggesting that the Early Triassic played host to a rapid expansion of stereospondyls, possibly filling the role of “disaster taxa” as they succeeded where other amphibians and amniotes dropped in species number. The decline toward the end of the Triassic is in spite of the presence of TBFF and finds of other tetrapods would indicate that the majority of stereospondyls did not survive the end Triassic extinctions. The closer inspection of Australian TBFF highlighted the lack of fossiliferous formations, which allows support for the argument that the presence of two Brachyopoidea later in the fossil record is evidence of Australia being a refuge (Warren and Black, 1985). There are a plethora of studies that attempt to determine the reliability of the fossil record (see Benton, 2015), but this is not one of them. TBFF is a fairly basic approach to assessing fossil record bias, though it has allowed us to consider the general patterns of stereospondyl diversity in light of a proxy of fossil record bias.

3.4.6 Summary

In response to the original hypotheses, stereospondyls do not have an equal distribution in the fossil record across time and location. Europe and Africa dominate the stereospondyl fossil record and the Early Triassic was host to the most known species.

Stereospondyl genera do not persist in the fossil record for equal lengths of time, the Early Triassic taxa were short lived, many persisting for a single stage, where later and earlier taxa have persisted through several time bins, giving the Early Triassic taxa the impression of a high turnover. The stereospondyl fossil record is not biased by stage duration or fossil completeness but it is biased by tetrapod bearing fossil formations, the latter of which encompasses rock availability, preservation bias and researcher effort. These biases are driven largely by the poor preservation of southern sites and the Middle Triassic, stereospondyls exceeded predicted diversity in the Early Triassic and fall below predicted diversity in the Late Triassic.

The Early Triassic was clearly an important period in stereospondyls evolutionary history. The species seemed to be able to tolerate high temperatures, and perhaps rapidly diversified in to empty niches though these genera were short lived. In the presence of more stable environments in the Middle Triassic, competition from other tetrapods may have increased, as stereospondyl originations decreased, though their genera were longer lived, persisting through multiple stages. This conclusion is tenuous due to poor fossil records in the Middle Triassic. Finally the stereospondyls largely disappeared from the fossil record, becoming extinct in line with the multiple extinctions of the Late Triassic, leaving only a small refuge population in Australia.

From these data it can be confidently stated that the distribution of stereospondyls in the fossil record changes with both time and location, and thus climate and ecosystem. The question remains, why? To answer this question the following chapters will quantitatively examine the distribution of functionally informative shapes amongst stereospondyls.

Chapter 4: Geometric Morphometrics of Stereospondyl Skull Features

4.1 Introduction

4.1.1 Overview

Geometric morphometric analysis is a quantifiable method of capturing the amount of shape change between individuals and groups. Where previous qualitative approaches have been used to describe differences and changes, this approach is objective and repeatable (Fortuny et al., 2011, Polly et al., 2016, Penrice and Ruta, 2017), allowing for consolidation of a great amount of information taken from the same material. There is substantial mathematical theory to support the use and scope of geometric morphometrics (Polly et al., 2016), making it useful for groups where there is considerable morphological variation, such as the stereospondyls.

Polly et al., (2016) provide a comprehensive review of the theory and methods of geometric morphometrics. The main elements are that principal components of Procrustes coordinates (size and rotation adjusted coordinates from landmarks) produce a multivariate shape space, commonly referred to as a morphospace. The position of the objects (in this case anatomical features of species) is based on the similarity or differences in their shapes, allowing similarities and differences between the individuals to be visualised and analysed.

Geometric morphometrics can be used to analyse disparity (shape differences) between species and individuals in cases where a discrete analysis, such as a character state analysis, is either inappropriate or uninformative, or in conjunction with them. Geometric morphometric analyses of shapes can be viewed in terms of discrete categories, such as taxonomic groups, to identify changes in morphospace occupation. For example, the occupation of species in a morphospace is an effective way to look at shape changes through time (Laffont et al., 2011). The mathematical transformations that are necessary to turn shape into a morphospace also remove the effect of size, as the shapes are all scaled to the same proportions. Stereospondyls have a huge size range, and this can dominate morphometric analyses. By removing the effect of size, I may be able identify further structural differences that would have been missed with the confounding effects of allometry (Leonart et al., 2000).

Disparity studies can be done in several ways, such as traditional linear morphometrics, but this limits analysis to two measures at a time. As a more encompassing approach, geometric morphometric analysis provides a tool to quantify the degree of change between individual taxa based on occupation of morphospace (Stayton and Ruta, 2006). Organisms can be assessed as whole, or a set of individual elements or features defined as landmarks. Geometric morphometrics allow shapes to be assessed on a continuous scale rather than as a series of predefined discrete categories.

4.1.2 Geometric morphometrics in palaeontology

The assessment of shape is worth exploring because engineering plays just as important a role as evolution in shape determination (Polly et al., 2016). The physical demands of the environment could have some influence on shape, a basic example being the shape of the head in an aquatic or terrestrial environment. Despite the efforts of palaeontologists, the allocation of fossil finds to phylogenies and life histories is in constant flux (Benton et al., 2013) partly because phylogenies contain a component of subjective characters, selected at the authors' discretion. The use of shape is, therefore, valuable because it is independent of many of these subjective arguments. Methods like Maximum Parsimony that are used to construct phylogenies seek to reduce changes between taxa, whereas Principal Component analysis seeks to demonstrate the largest sources of change.

In many phylogenetic studies morphological elements have been described in broad categories. For example, Schoch and Witzmann (2009) described pre-orbital skull shape in stereospondyls as two character states: 0 – less than twice the length of the posterior skull table, and 1 – more than twice the length of the posterior skull table. This approach, although it has its uses, is inherently restricting because it places all stereospondyls into one of two categories to describe a part of the skull that demonstrates considerable variation. It is common for characters to have only two states, although it is rare, characters can have as many as four. By restricting the analysis of highly variable characters to a fixed number of states, a lot of information about the anatomy of the individual or species can be lost. The potential differences between the degrees of curvature is much more substantial than can be attributed to two categories.

Another challenge with phylogenies in palaeontology is the prevalence of subjective characters used for phylogeny reconstruction. For example, Steyer (2002) categorised the posterior skull margin of stereospondyls into two states: 0) slightly concave or 1) semi-

circular. It is left to the reader to determine where the distinction is drawn. This can be a problem in any analyses, where one user might select 0 and another might select 1 for the same character on the same species, and so alter the shape of the resulting phylogeny, it can also be problematical where species descriptions are concerned because it leaves the distinction between species blurred, and easy to misinterpret. Objective shape analysis can help overcome this by removing the potential for user discrepancy.

Disparity studies can show some interesting and unexpected finds. Prentice et al. (2011) found differences morphospace occupations across time of pterodactyloids. The earlier species occupied a smaller and separate morphospace compared to the derived species. This study did not use the greatest range of information available from the shape, as it used differences between discrete characters to build a morphospace. The family differences found by the authors are no surprise in this case, since family relationships were constructed on the same characters, but the differences between species over time are an interesting insight gained by assessing shape over time. Changes in morphospace occupation across time has also been found among the Ichthyosaurs, but again it was based on discrete characters (Thorne et al., 2011). These two studies highlight the scope to expand the use of more “encompassing” disparity studies in palaeontology, where all parts of the shape are included, and not just assigned to one of two categories. By using shape and not character descriptions that are biased to retrieve family associations, we can determine if the morphometric differences are sufficient to distinguish taxonomic group or if the functional signals of morphology outweigh the taxonomic ones. As we know from chapter 3 the distribution of stereospondyls groups across time is not even, so we can examine the change in shapes across their taxonomic groupings which is indicative of time.

There is a clear link between the form of a shape and its function (Fortuny et al., 2011) and geometric morphometrics can be a useful tool to determine how one interacts with the other (Fortuny et al., 2011). Morphospace positions can differentiate functional and taxonomic similarities and differences (Sanchez et al., 2010) but in a quantitative, rather than a qualitative and subjective manner. In dinosaurs, limb bones have been shown to change their shape to adapt to function and this has been used to infer posture and locomotive patterns (Bonnan, 2007). Hence, morphospace occupation can be used in conjunction with additional information, such as environment or time period, to infer life history traits and differences in functional characteristics of major clades (Fortuny et al., 2011).

4.1.3 Geometric morphometric studies of stereospondyls

Stereospondyls exhibited a range of morphotypes and have been the subject of a small number of geometric morphometric studies (Stayton and Ruta, 2006; Fortuny et al., 2011). Stayton and Ruta (2006) showed that stereospondyls occupy areas of morphospace based on a range of morphological characteristics of the skull roof in dorsal view, based on 22 discrete landmarks of 62 species. They stated that morphological concordance with phylogenetic distance was poor, excepting the phylogeny of Yates and Warren (2000), though there was some grouping in morphospace by the taxonomic groups. However, there is a considerable amount of available material for stereospondyls that was not utilised in this analysis. For example, suture points and skull shape differences, as well as a range of characteristics on the entirety of the palate, have not been explored using geometric morphometric techniques. Fortuny et al., (2011) also recovered the main taxonomic groups in morphospace using 17 discrete landmarks of the skull roof of 17 temnospondyls to complement FEA (Finite Element Analysis) of the skull roof.

Since functional interpretation is generally lacking in clade-wide studies of stereospondyls, further objective analyses of skull roof and palatal elements may yield greater insight into scalable, rather than discrete changes in functional morphology. For instance, the arrangement of bones around the orbit could play a role in the absorption of forces during feeding (Kathe, 1999), or they may not vary in any significant manner. Orbit size and position did not affect the overall strength of the stereospondyl skull, but von Mises Stress values from FEA showed the level of the orbits are the location of the greatest strain on the skull (see Marce-Nogue et al., 2015).

The analysis described in this chapter deals with geometric morphometrics of the whole skull and a series of key structures or bones within the skull. These are perceived as having a degree of functionality – skull shape may reflect patterns of prey acquisition, or the shape of the subtemporal vacuity indicates the maximum extent of jaw muscle as it passes through the vacuity (Yates, 1999; Steyer, 2002; Fortuny et al., 2011). Other features are specific skull roof bones, which were chosen for their role in phylogenetic studies or for their functional properties. The reasons for selecting some but not all structure are discussed below.

The lacrimal bone of the skull roof features in several studies of stereospondyls (Figure 4.1; Damiani and Warren 1996; Yate and Warren, 2000; Warren and Marsicano 2000;

Damiani, 2001; Schoch, 2006; Schoch et al., 2007; Schoch and Witzmann, 2009, Dias da Silva and Marsicano 2011). The lacrimal is of interest because it exhibits highly variable morphology and it is not always present in the skull table (it is occasionally found underneath the prefrontal bone (Schoch, 2006)). The function of the lacrimal is not clear, but the more detailed analysis done here, could reveal a pattern in morphospace that helps to infer its purpose, if it has one. It may simply be an artefact of skull shape changes. If the lacrimal shows a similar morphospace occupation to another feature, such as the orbit, or the skull outline, we may be able to suggest its function. If it varies with the orbit then it likely had a role in supporting the orbit, if it varies with the skull shape, it may play a role in supporting the mid orbital skull table.

The tabular bone forms part of the otic notch / squamosal embayment (Damiani, 2001; Fortuny et al., 2011), an embayment on the posterior skull margin that is quite plastic in its morphology, though the full closure (creating a circular foramen), seems to occur only once, in the *Capitosauroida* (Schoch, 2000). Many authors have included it in their phylogeny analyses (Damiani and Warren, 1996; Marsicano, 1999; Yates, 1999; Bolt and Chatterjee, 2000; Schoch, 2000; Yates and Warren, 2000; Damiani, 2001; Steyer, 2002; Steyer, 2003; Schoch et al., 2007; Schoch, 2008; Schoch and Witzmann, 2009; Dias da Silva and Marsicano, 2011; Warren et al., 2011; Maganuco et al., 2014). Sulej and Majer (2005) suggested that the tabular was connected to the clavicle via a muscle to create a skull raising system in the *Capitosauroida*. A posterior extension of the tabular would create a lever arm for this muscle, increasing the efficacy of the muscle, as would an increase in the inter-tabular distance (Sulej and Majer, 2005). The morphological disparity of the tabular makes it very difficult to characterise with words, as in the typical matrix-based phylogeny studies, so it is an ideal candidate for a quantitative analysis.

The subtemporal vacuity is where jaw muscles pass through the palate from the skull to the mandible, and both its size and shape are important. The shape of the subtemporal vacuity influences feeding action as it will dictate much of the lateral movement of the lower jaw, where a wider posterior subtemporal vacuity would allow the lower jaw a greater lateral reach or overall gape (Yates, 1999). A wider or longer shape would allow for additional musculature to pass through, particularly enlarged anterior or posterior adductor muscles (Damiani, 2001) which would create an anchor for the jaw, securing a prey capture. The presence of a downturned flange on the palatine ramus of the pterygoid, which shapes the anteromedial border of the subtemporal vacuity, can provide extra support for muscles that can create a rapid and hard initial bite (Yates, 1999).

Unfortunately, to determine its presence, the skull needs to have a well-preserved palate, which are not common amongst stereospondyl finds. In a two-dimensional plane there is still a lot that can be inferred from the shape. For example, a long and narrow shape would indicate reduced lateral movement, or a triangular shape would show a greater proportion of strength at a different point of the bite and suggest which of the jaw adductor muscles were largest (see Figure 4.3 in methods). The jaw is discussed further in chapter 6.

Aside from improving our understanding of the functional properties of structures, a secondary element of analysing skull shapes is their role in phylogeny reconstruction. Stayton and Ruta (2006) found discrete landmarks on the skull roof could be used, to some extent, to distinguish between taxonomic groups of stereospondyls. However, when morphological distance was tested against phylogenetic distance from published phylogenies, they argued that concordance between morphology and phylogeny was poor, though this places heavy emphasis on the phylogenies being accurate. There was some morphological convergence within the taxonomic groups, as was shown by Fortuny et al., (2011). Both of these studies used geometric morphometrics of the skull roof bones for their morphological disparity assessment. To date, no geometric morphometric studies have used palatal elements, despite the heavy reliance on palatal features in phylogeny assignments (see chapter 2).

4.1.4 Aims and Objectives

The aim of the study described in this chapter was to determine how variation in the morphospace occupation of functionally informative elements of stereospondyl skulls changed in relation to taxonomic group affiliations, and which elements of the skull were responsible for the most variation amongst stereospondyls. Geometric morphometrics allowed for the examination of overall shape and position of physical features, controlling for the effects of size. A two-dimensional morphospace was created, and the analysis positioned taxa within this space according to their similarities and differences. Although 3D skull data could be more informative, stereospondyl skulls are dorsoventrally flattened, and using two dimensional shapes meant that images from literature could be used when the specimens were not examined first hand, which increased the data available. The results provided insight into the elements that showed the most variation, and differences between taxa could be analysed based on their occupation of morphospace.

Two approaches were used to show the greatest sources of shape variation in the stereospondyl skull. Firstly, discrete landmarks, as used by Stayton and Ruta (2006) and Fortuny et al., (2011), of the skull roof and palate. These are x-y coordinates of features that are independent of each other but mark the position of the nares, orbit, and suture joints. This approach demonstrates the relative positions of these features, as well as the generalised shape. The subsequent principal components analysis will show which one of the shape changes was the source of greatest variation between species. By using this approach, it can be determined whether many of the two-dimensional morphological characteristics that are used in phylogenetic studies are actually the same features that are responsible for much of the variation between individual species. Secondly, semilandmarks were used, which are a sequence of coordinates positioned along an edge of a morphological feature. A fixed number of x-y coordinates are evenly spaced around a silhouette, which are used to analyse the outline of the skull and a selection of anatomical features. This approach, never used on stereospondyls, encompasses all elements of the two-dimensional shape, giving much more information to the shape, than the previously mentioned dichotomous characters. The greater detail of the shape, as well as its objective nature, will demonstrate where the greater differences between the shapes lie. These geometric morphometric techniques were used here to quantify the greatest source of shape variation in aspects of stereospondyl skull anatomy.

Given that we know there were differences in climate over time, and different stereospondyl populations in different continents, it raises the question of whether this is reflected in any clear occupations of morphospace of functionally informative anatomy, when species are delimited by taxonomic affiliations. Additionally, the skull shape variation in dorsal view was compared between stereospondyls and a range of extant amphibians. Extant amphibians are known to inhabit a range of ecological niches but, superficially, appear to have more conservative skull morphology than stereospondyls. This will help to underpin the comparative anatomy chapter (Chapter 6).

Hypotheses

- 1) Stereospondyl groups will be clearly delimited in morphospace by their skull roof anatomy as morphology is the basis for taxonomic affinities
- 2) Stereospondyl groups will be clearly delimited in morphospace by their palate anatomy
- 3) Skull shape correlates with orbit shape as orbit shape is not independent of skull shape

- 4) Skull shape correlates with naris shape
- 5) Extant amphibians can be clearly delimited in morphospace as anurans, urodeles and caecilians
- 6) Stereospondyls exhibit more skull shape variation in dorsal view than extant amphibians

4.2 Methods

4.2.1 Taxa selection

For each character explored taxa were selected on the basis that all landmarks, or semilandmarks, were present for the feature under examination. A full list of which taxa, and their taxonomic affiliations, were used in each of the analyses is available in Appendix EA2. Every effort was made to maximise the taxa used and to ensure representative taxa were used from all taxonomic groups. Original photographs formed the basis of the analyses for most of the taxa described here but where they were not available, then reconstructions from literature were used (EA2). Extant amphibians were selected to encompass a range of families, totalling 34 species from 19 families (Electronic Appendix EA4). Images were analysed in dorsal aspect and sources from the Digimorph project (Digimorph.org) and Wilkinson et al. (2011).

4.2.2 Recording of landmarks

The geometric morphometric analyses were based on a series of digital landmarks superimposed on images of stereospondyl skulls, which were recorded as *x-y* coordinates. Ten different analyses were carried out (see Table 4.1), to encompass the overall differences between stereospondyl skulls, and between specific characteristics. These analyses used both semilandmarks and discrete landmarks. Discrete landmarks are independent of each other and can be placed in any order that the user wishes. By contrast, semilandmarks are positioned in relation to the landmarks that are before and after it, a predetermined number of semilandmarks were evenly spaced around an object.

In all cases, except for the skull outline, the right hand side of the skull was used because of the assumed symmetry of the skull landmarks (Schneider et al., 2012). In cases where this was not preserved but the left-hand side was intact, the image was flipped using a GNU Image Manipulation Program (GIMP 2.8.16). Using the entire skull would have limited the number of taxa that could have been included without significant photograph

manipulation, and since the skulls are symmetric, using half of the skull for discreet landmark analysis was deemed sufficient.

The discreet landmarks were used for two analyses, a complete skull roof analysis and a complete palate analysis. To do this, landmarks were selected to complement the earlier work of Stayton and Ruta (2006) and Fortuny et al., (2011). The positions and descriptions of the landmarks are shown in Figure 4.2 and Table 4.2. New landmarks (not in the literature) encompass additional suture joints between bones, as well as points on the outer edges of the skull table. The palatal landmark details are illustrated in Figure 4.3 and described in Table 4.3. As with the skull roof landmarks, the landmarks were selected to encompass the suture joints and the extremities of bones and vacuities.

Semilandmarks were used to analyse the differences in skull outlines and outlines of select orifices and bones (Table 4.1). Images used in the semilandmark analysis were first turned into silhouettes in GIMP software to produce a black foreground and white background. This allowed the use of automatic outline detection in TPSDIG2 (ver. 2.17; Rohlf, 2005). With the skull image orientated with the snout uppermost (as in Figure 4.1) the landmarks were automatically digitised and equally spaced in an anticlockwise direction from the centre of the anterior most point of the skull or character.

In all analyses, x , y coordinates were exported from ImageJ or TIPDIG2 as a text file. These files were then compiled into master text files containing all of the appropriate taxa, one for each of the analyses described in the Table 4.1. These data were then imported into MorphoJ for morphospace analysis.

4.2.3 Analysis

For all analyses, a procrustean superimposition was first carried out in MorphoJ (Klingenberg, 2011). Procrustean superimposition is an orthogonal transformation using sum of squares of shapes. It centres all shapes at an origin (0, 0), then rotates them around this origin, so that the sum of squares differences between the landmarks is minimised, and scales all of them to a unit scale (Rohlf, 2006). This removes the cumulative effects of size and rotation. The results is that the x , y coordinates from the landmarks are reflective of pure shape differences between different taxa.

Within MorphoJ a variance-covariance matrix was produced from the coordinates, which was then used for principal components analysis (PCA; Klingenberg, 2011). PCA is a useful technique to show patterns in data (Smith, 2002). PCA is an orthogonal transformation multivariate analysis technique that seeks the shortest distances between

two points (Wold et al., 1987). Using covariance means that the analysis is two dimensional, and the data (the landmarks) can be examined in relation to each other (Smith, 2002). The covariance matrix provided the foundations for the eigenvector and eigenvalue calculations within the PCA. The eigenvector is the direction of the line of most variation, the eigenvalue is the variance of the data in that direction. The resulting PC scores showed the relative position of taxa in morphospace. The first PC is the one that encompasses the most variation between the taxa. It is the direction where the distance is greatest, based on eigenvalues and eigenvectors.

Scree plots (see Figure 4.4 for an example) were used for interpreting the first two principal components of each analysis. Where the variances of PC1 and PC2 were less than 50% cumulative, then PC3 was also explored. The scree plots show a centre point, which is the average position of each landmark (centroid), and a line, the size of which is in proportion to the magnitude of the variation (scalable vectors). The direction of the line shows the orientation of change for that PC. The further along the positive direction of the PC axis, the further down the “line” of the scree plot (away from the centre point) an individual taxon are.

Principal component (PC) scores were exported as a text file and subjected to permuted multiple analysis of variance (PERMANOVA) and analysis of similarity (ANOSIM), both with 9999 permutations in PAST v. 2.17c (Hammer et al., 2001). Pairwise comparisons were carried out using straight line Euclidean distances (Deeming and Ruta, 2014, Penrice and Deeming, 2016). In these analyses the taxa were categorised by group and statistical tests were carried out on PC1 and PC2.

PERMANOVA produces F and P values, with the same principles as the ANOVA (Anderson, 2001), using distance measures to test for variance differences between groups. The significance of both tests results from 9999 permutations of group membership. ANOSIM uses the mean rank of all distances between group and the mean rank of distances within groups to test for similarity, producing an R and P value. R is between 0 and 1, where a value of 1 indicated complete dissimilarity between the groups (Clarke, 1993).

Sequential Bonferroni correction, also known as the Holm-Bonferroni correction, was applied to control the issue of multiple comparisons (Holm, 1979). It alters the rejection threshold of statistical analyses to reduce the likelihood of a Type I error.

To determine correlation between morphospaces, and so correlation between characteristics, Mantel tests were used, which assess correlation between straight line distances of matrices. This allowed the determination of whether certain feature changes may be auto correlated with other features, for example naris and orbit shape, and skull outline and orbit shape.

Extant amphibians were subjected only to the skull outline analysis as their skull bone composition is not directly comparable to stereospondyls. A lateral silhouette outline analysis would be uninformative here as the results would be biased by the substantial differences in skull depth.

Table 4.1 Details of the number of species and type of landmarks for the geometric morphometric studies

Anatomy	Number of taxa	Landmarks
Skull roof	77	41 discreet
Palate	33	31 discreet
Skull outline	114	250 semilandmarks
Orbit	119	40 semilandmarks
Naris	95	40 semilandmarks
Ectopterygoid	63	40 semilandmarks
Lacrimal	77	40 semilandmarks
Palatine	60	40 semilandmarks
Subtemporal vacuity	70	40 semilandmarks
Tabular	114	40 semilandmarks

Table 4.2 Skull Roof landmark numbers and descriptions as illustrated in Figure 4.2

Number	Description
1*	Anterior extremity of suture between premaxillae (tip of the prenasal region of the snout)*
2*	Anterior extremity of the suture between the nasals*
3*	Lateral extremity of the suture between the premaxilla and nasal (its intersection with the nostril margin)*
4	Lateral edge of the skull table at the level of the mid nostril
5	Anterior most point of the nostril margin
6	Posterior most point of the nostril margin
7	Medial most point of the nostril margin
8 [¥]	Lateral most point of the nostril margin
9	Lateral extremity where the nasal enters the narial border
10	Anterior extremity of the suture between the prefrontal and the nasal
11*	Anterior extremity of the suture between the frontals*
12	Triple junction between the prefrontal, nasal and frontal
13 [¥]	Anterior extremity of the suture between the prefrontal and the jugal
14	Lateral extremity where the prefrontal enters the orbital margin
15	Medial extremity where the prefrontal enters the orbital margin
16	Posterior most point of the maxilla on the skull margin
17*	Anterior most point of the orbital margin*
18*	Posterior most point of the orbital margin*
19*	Medial most point of the orbital margin*
20*	Lateral most point of the orbital margin*
21	Lateral edge of the skull table at the level of the mid orbit
22	Anterior extremity of the suture between the frontal and post frontal
23*	Anterior extremity of the suture between the parietals*
24*	Triple junction between the frontal, postfrontal and parietal*
25	Lateral extremity where the postorbital enters the orbital margin
26	Medial extremity where the postorbital enters the orbital margin
27*	Anterior end of the pineal foramen*
28*	Posterior end of the pineal foramen*
29*	Anterior extremity of the suture between the postparietals*
30*	Posterior extremity of the suture between the postparietals (posterior margin of the skull table)*
31*	Triple junction between postfrontal, supratemporal and parietal*
32*	Triple junction between postfrontal, supratemporal and postorbital*
33*	Triple junction between postorbital, supratemporal and squamosal *
34*	Triple junction between postorbital, jugal and squamosal*
35*	Triple junction between quadratojugal, jugal and squamosal*
36*	Intersection between postparietal-tabular suture and the posterior margin of the skull table*
37	Triple junction between the postparietal, parietal and the supratemporal
38	Triple junction between the postparietal, supratemporal and the tabular
39 [¥]	Posterior extremity of the suture between the supratemporal and squamosal
40	Posterolateral extremity of the tabular
41	Intersection between squamosal-tabular suture and the posterior margin of the skull table
42	Lateral edge of the tabular where it meets the skull margin
42	Posterior extremity of the squamosal and quadratojugal suture (adapted)
43	Lateral edge of the skull table at the level of the posterior extremity of the post parietal sutures

*denotes landmarks from Stayton and Ruta (2006), [¥] denotes landmarks used by Fortuny *et al.* (2011).

Table 4.3 Number and description of 31 discrete landmarks used in the analysis of the palate as illustrated in Figure 4.2.2.

Number	Description
1	Anterior extremity of suture between premaxillae (tip of the prenasal region of the snout)
2	Lateral edge of the anterior palatal vacuity/fossa
3	Anterior extremity of the vomerine suture
4	Posterior extremity of the vomerine suture
5	Anterior extremity of the maxilla on the skull margin
6	Antermost point of the choana
7	Posteriormost point of the choana
8	Medialmost point of the choana
9	Lateralmost point of the choana
10	Anterolateral most point of the palatine
11	Anteromedial most point of the palatine
12	Medial extremity of the suture between the palatine and ectopterygoid
13	Lateral extremity of the suture between the palatine and ectopterygoid
14	Lateral point of the widest part of the ectopterygoid
15	Medial point of the widest part of the ectopterygoid
16	Posterolateral extremity of the ectopterygoid
17	Anterior extremity of the pterygoid
18	Antermost point of the interpterygoid vacuity
19	Posteriormost point of the interpterygoid vacuity
20	Medialmost point of the interpterygoid vacuity
21	Lateralmost point of the interpterygoid vacuity
22	Posterior extremity of the maxilla on the skull margin
23	Anterior extremity of the suture between the pterygoid and parasphenoid
24	Posterior extremity of the suture between the pterygoid and parasphenoid
25	Mid-point between the exoccipitals on the parasphenoid
26	Posterior extremity of the exoccipital
27	Posterolateral extremity of the pterygoid (quadrate ramus)
28	Anterior most point of the subtemporal vacuity
29	Posterior most point of the subtemporal vacuity
30	Medial most point of the subtemporal vacuity
31	Lateral most point of the subtemporal vacuity

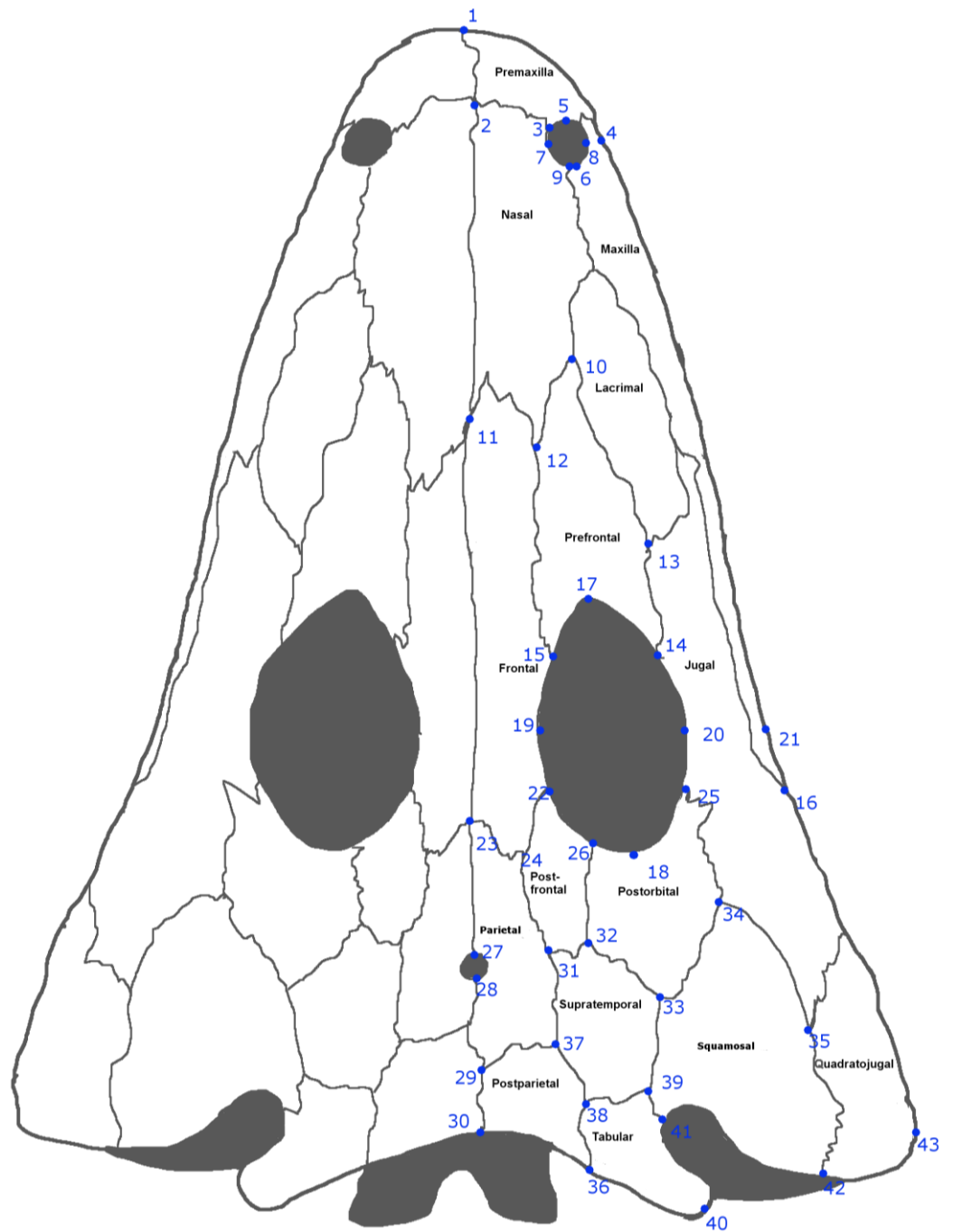


Figure 4.1 Reconstruction of *Mastodonsaurus giganteus* in dorsal view, the anterior of the skull is at the top of the page. Blue circles show the positions of the 43 landmarks used for skull roof morphometric analysis, which correspond with the descriptions in Table 4.2. The shaded areas within the skull roof are the nares (anterior) and orbits. The shaded areas at the posterior skull margin are elements of the exoccipital that are visible in dorsal view.

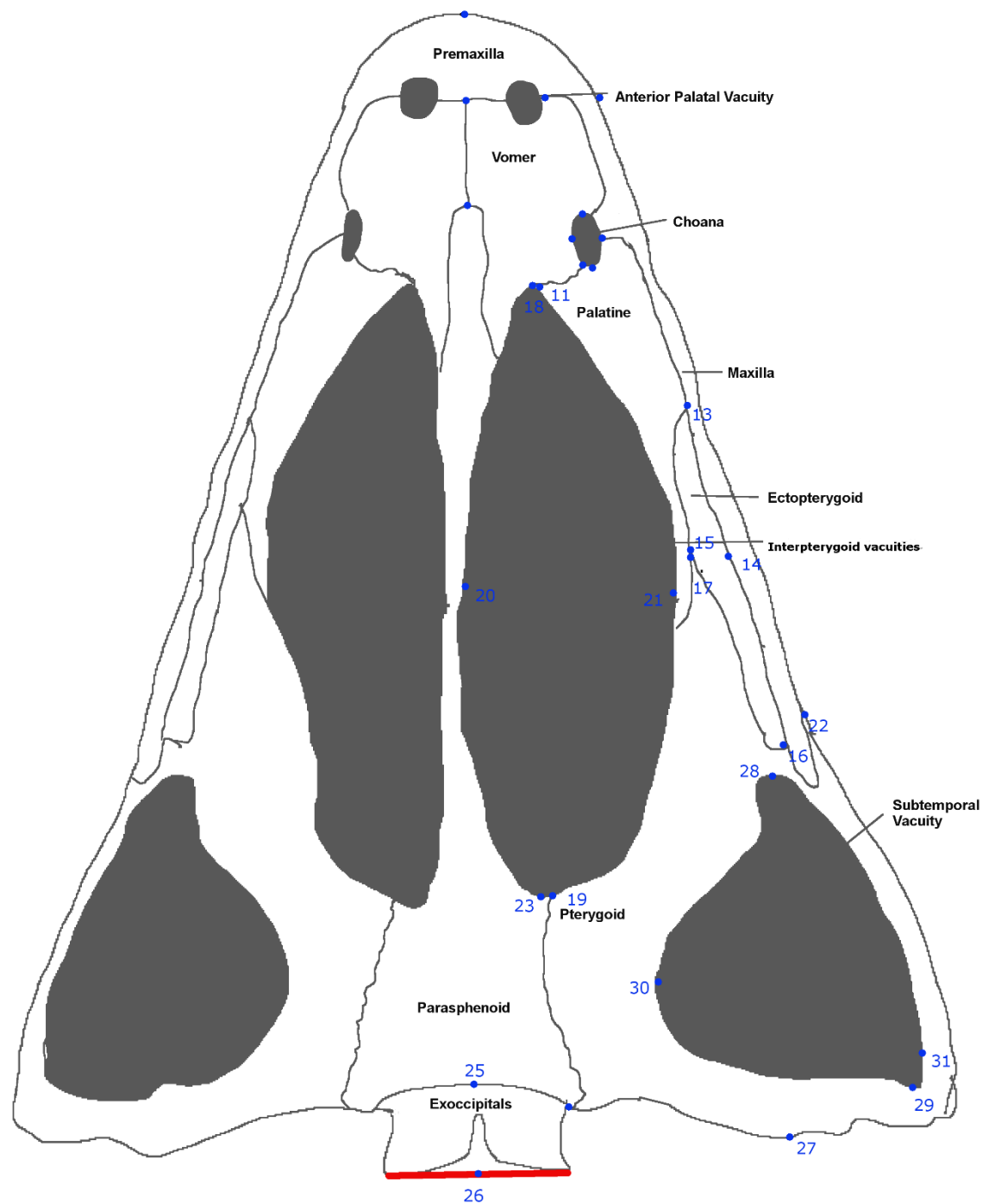


Figure 4.2 Reconstruction of *Mastodonsaurus giganteus* in ventral view, the anterior of the skull is at the top of the page. Blue circles show the positions of the 31 landmarks used for palatal morphometric analysis as defined in Table 4.3. The shaded areas are vacuities in the palate, as labelled.

4.3 Results

4.3.1 Skull roof described by discrete landmarks

The first two principal components accounted for more than 60% of the variation in the skull roof (Figure 4.3). The first Principal component (PC1) accounted for 47% of the variance in the skull roof discrete landmark positions. Scree plots for the first two principal components, showing the location and magnitude of the changes are also shown in Figure 4.3. PC1 showed greatest variation in the position of the orbits, which varied in on anterior-posterior axis, moving anteriorly along the positive direction of PC1. By contrast, the naris showed most variation in a posterior direction. There was a slight lateral spreading of the landmarks in the postorbital skull table that would make this area wider (Figure 4.3). PC2 showed variation that indicated an overall lengthening and narrowing of the skull features, particularly around the mid skull region anterior to the orbit (Figure 4.3).

A scatterplot of PC1 and PC2 revealed a relatively tight cluster of points in the centre, with some outliers for both axes (Figure 4.4; scatterplots with labelled data points are in Electronic appendices A 3). Levene's test showed a significant difference between the variance of taxon along the PCs ($F = 33.012$, $p < 0.0001$). At the most positive part of the range of PC1 were the wide-headed *Gerrothorax* (Plagiosauridae), and the metoposaurs (a group within the Trematosauroidae, Schoch and Milner, 2000; Witzmann and Schoch, 2006), characterised by eyes that are relatively further forward and more laterally placed (Figure 4.4). Superficially this appears to be a result of a change in rostrum length, however, closer examination of the shape changes on PC1 shows that as the orbits move forward, the posterior skull margin moves backward, increasing the overall size of the posterior skull table, so the orbits are moving forward, not just showing the effects of a smaller rostrum (Figure 4.4). Here the distance between the pineal foramen and the posterior margin of the skull allows determination of whether the orbits are moving forward relative to the pineal foramen or whether the post foramen skull is getting larger. The genus *Parotosuchus* had several species at the negative extreme of PC1, their skull shape is characterised as an isosceles triangle, with small orbits toward the posterior of the skull table. For PC2 there seemed to be most variation in skull elongation and snout narrowing. The extreme positive values for PC2 were associated with several of the long-snouted trematosauroids, such as *Tertrema acuta* (Figure 4.4) whereas the very short-snouted *Gerrothorax* was the most negative taxon on PC2.

PERMANOVA ($F = 22.17$, $P = 0.0001$) and ANOSIM ($R = 0.608$, $P = 0.0001$) showed that there were significant differences between stereospondyl species from different taxonomic groups (Table 4.4). Taxonomic group separation showed the clear differences between the landmarks of the skull roof (Figure 4.5) but the Brachyopoidea were not represented in the analysis of taxonomic group as they lacked the well-preserved skull roof needed here. ANOSIM and PERMANOVA both showed that the Capitosauroidae were significantly different from all other taxonomic groups (Figure 4.5, Table 4.4) and were characterised by greater distances between the orbits and nares as they occupy a negative position on PC1. Differences were found between the Rhytidosteoidea, which had less distance between their orbits and nares, and all groups except the stem stereospondyls when correction is applied. The Trematosauroidae differed from the Archegosauridae and stem stereospondyls but only when there is no correction applied. The Trematosauroidae showed the most within group variation for the distance between the orbits and nares, driven by the inclusion of the metoposaurs.

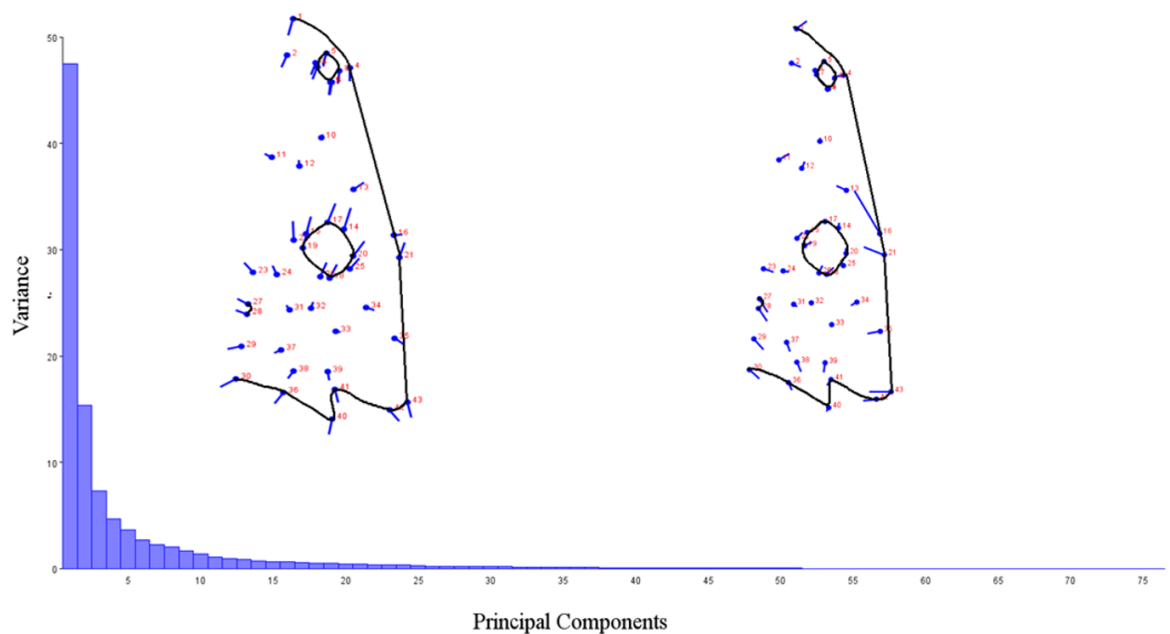


Figure 4.3 Variance explained by the Principal components of 43 discrete landmarks on the skull roof of 77 stereospondyl species. Scree plots of PC1 (left) and PC2 (right) are shown, with the anterior portion of the skull toward the top of the page and the orbit (centre), naris (top), and right side of the skull shown in shape. Landmarks correspond with those shown in Figure 4.1 and defined in Table 4.2

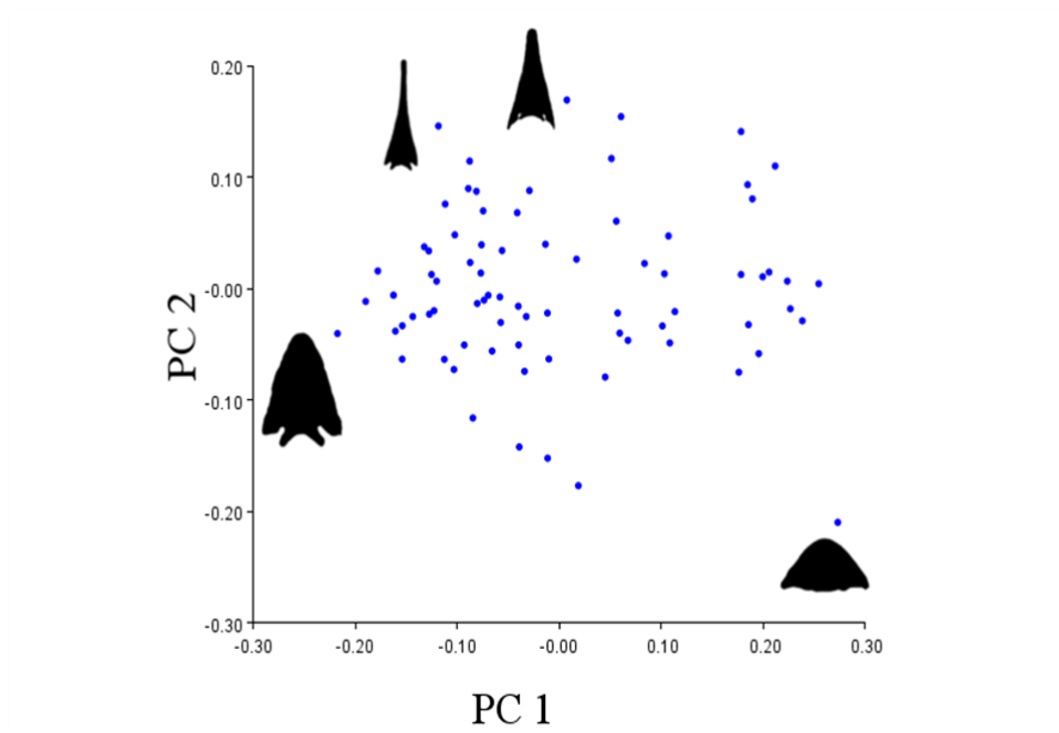


Figure 4.4 Position in morphospace of 77 stereospondyl species, along PC1 and PC2 based on the position of 43 discrete landmarks on the skull roof. Skull shapes of *Gerrothorax pulcherrimus* and *Parotosuchus orenburgensis* are illustrated at the most positive and negative positions on PC1, respectively. *Tertrema acuta* (top right) and *Aphaneramma rostratum* (top left), represent the positive PC2 skull shapes. Fully labelled diagrams are in electronic appendix EA 3.

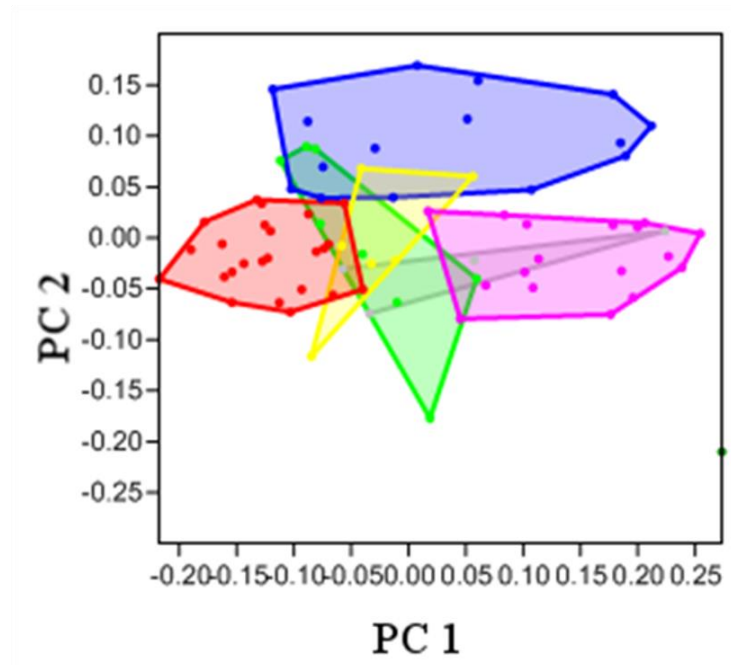


Figure 4.5 Position in morphospace of 77 stereospondyl species based on the position of 43 discrete landmarks on the skull roof, with convex hulls delimiting the taxa as categorised according to their taxonomic group affiliation (as per Schoch and Milner, 2000): Archegosauridae - bright green, Trematosauroidae - blue, Rhinesuchidae - yellow, Stem stereospondyl - grey, Rhytidosteoidea - pink, Capitosauroidae - red, Plagiosauridae - dark green (single point).

Table 4.4 Pairwise comparisons of PC1 and PC2 scores of skull roof discrete landmarks, designated by taxonomic group. PERMANOVA values are above the diagonal and ANOSIM values are below the diagonal. Bonferroni sequential corrected significant values are indicated in bold.

Abbreviations are as follows Stem = Stem stereospondyls, Arch = Archegosauridae, Brachy = Brachyopoidea, Plag = Plagiosauridae, Tremat = Trematosauroidae, Rhine = Rhinesuchidae, Rhyt = Rhytidosteoidea, Capit = Capitosauroidae

	Stem	Arch	Tremat	Rhine	Rhyt	Capit
Stem		0.1859	0.0607	0.2769	0.047	0.0002
Arch	0.2561		0.0056	0.9422	0.0001	0.0022
Tremat.	0.0175	0.0407		0.0222	0.0001	0.0001
Rhine	0.3905	0.5716	0.1121		0.0001	0.0001
Rhy	0.0144	0.0001	0.0001	0.0001		0.0001
Capit	0.0004	0.0001	0.0001	0.0002	0.0001	

4.3.2 Palate described by discrete landmarks

In contrast to other PCA analyses reported here the proportion of variance explained by higher value principal components was much lower. Hence, the first two PCs for palatal discrete landmarks explained only 47% of the variation seen across the landmarks on the palate (Figure 4.6). PC1 accounted for 32% and PC2 15%, PC3 was not much lower at 10%, so it was included in these analyses. Variation in PC1 showed a general widening of the skull and large interpterygoid vacuities, with the subtemporal vacuities widening laterally (Figure 4.6). The landmarks at the anterior of the palate, representing the choana and anterior palatal vacuity, amongst others, exhibited most variation in the posterior axis indicating a shortening of the snout.

A plot of PC1 and PC2 (Figure 4.7) showed a central cluster, as with most morphospace analyses, but there was a wide spread around this, suggesting that there was no “typical” stereospondyl palate, and there was much variation in the palate as there is in the dermal skull roof. Levene’s test showed no significant difference between the variance distribution of species along the axes ($F = 2.689$, $P = 0.105$). The wide-headed Brachyopoidea, *Vigilius wellsi* occupied the most extreme positive position on PC1, the garial-like Archegosauridae *Platyoposaurus stuckenbergi* had the lowest PC1 score as

well as the highest PC2 score (see Figure 4.7; a fully labelled morphospace is in electronic appendix EA 3).

PC2 did not exhibit variation that indicated an overall direction of feature change as was seen with the narrowing on PC1, but individual landmarks showed considerable anterior and posterior variation. The anterior extremity of the maxilla on the skull margin (landmark 5), the medial point of the interpterygoid vacuity (landmark 20), and the lateral point of the interpterygoid vacuity (landmark 21), all exhibited significant variation in the posterior direction (Figure 4.6). By contrast, the posterior extremity of the vomerine suture (landmark 4), the anterior extremity of the pterygoid (landmark 17), and the posterior extremity of the maxilla on the skull margin (landmark 22), all exhibited most variation in the anterior direction. It appeared as though the maxilla exposure on the palate became shorter and the widest point of the interpterygoid vacuities was toward the posterior (Figure 4.9). *Platyoposaurus stuckenbergi* and *Australerpeton cosgriffi* occupied the most positive and negative positions along PC2, respectively, despite their similar skull shapes (Figure 4.10), the former had wider margins on the palate and the widest point of the interpterygoid vacuities was further posteriorly than the same point in *Australerpeton cosgriffi*. PC2 appeared to exhibit more variation in suture position than PC1 which is reflected in the difference between the two taxa.

PC3 exhibited greatest variation in the anterior direction for the position of the subtemporal vacuities and an overall narrowing of the anterior features (Figure 4.6), shown again by *Platyoposaurus stuckenbergi* which had a positive value for PC3 (Figure 4.7). A plot of PC1 and PC3 showed a widespread distribution of taxa along the PC3 and again no significant difference between the variance of species along the axis ($F = 5.536$, $p = 0.210$). The narrowing on PC3 was indicative only of the palatal features, and not the overall skull shape as trematosaur *Anaschisma browni* was also at the extreme positive end of PC3 (Figure 4.8).

PERMANOVA on PC1 and PC2 showed that there were significant differences between taxonomic groups ($F = 7.453$, $P = 0.0001$). With the addition of PC3 into the model, they remained significant ($F = 6.792$, $P = 0.0001$). ANOSIM of PC1 and PC2 showed significant differences between taxonomic groups ($R = 0.357$, $P = 0.001$) as did all three PCs combined. ($R = 0.4386$, $P = 0.0001$)

Stem stereospondyls, Brachyopoidea and Plagiosauridae were not represented in this analysis because of small samples. The Archegosauridae had little overlap with the other taxonomic groups and they occupied the most negative positions on the PC1 axis (Figure

4.9). PERMANOVA pairwise comparisons showed significant differences between Archegosauridae and the Trematosauroidae, Rhytidosteoidea and Capitosauroidae (Table 4.5). On PC1 and PC2, the Rhytidosteoidea and Capitosauroidae shared little common morphospace, the former occupied the more positive end of PC1 (Figure 4.8) and were significantly different from each other (Table 4.5). The Rhytidosteoidea were also significantly different from Trematosauroidae, which had a low position on PC2, and mid-range values on PC1 (Figure 4.9, Table 4.5). The outcome of the ANOSIM was similar, but there was no difference between Rhytidosteoidea and Trematosauroidae with this analysis (Table 4.5). The ANOSIM identified a further difference between the Capitosauroidae and the Trematosauroidae. When PC3 was included in the model, there was an additional pairwise difference between Rhinesuchidae and Trematosauroidae in the PERMANOVA and ANOSIM. There was no overlap between these two groups in the morphospace of PC1 and PC3. The addition of PC3 also saw differences between the Capitosauroidae and the Rhinesuchidae, the former occupied a more positive range on PC3 (Figure 4.9).

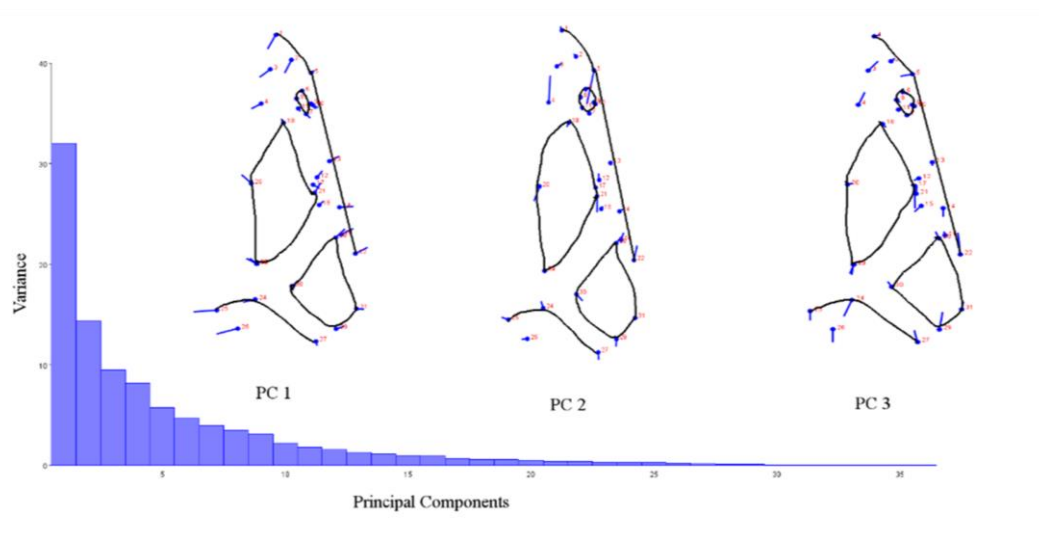


Figure 4.6 Variance explained by the principal components of 31 discrete landmarks on the palate of 36 stereospondyls. Scree plots of the first three principal components are shown with the anterior of the palate is toward the top of the page, with anatomical features, such as the large, central oval which is the interpterygoid vacuity, subtemporal vacuity at the bottom right and the choana at the top right, all outlined in black. Landmarks correspond with Figure 4.2 as defined in Table 4.3

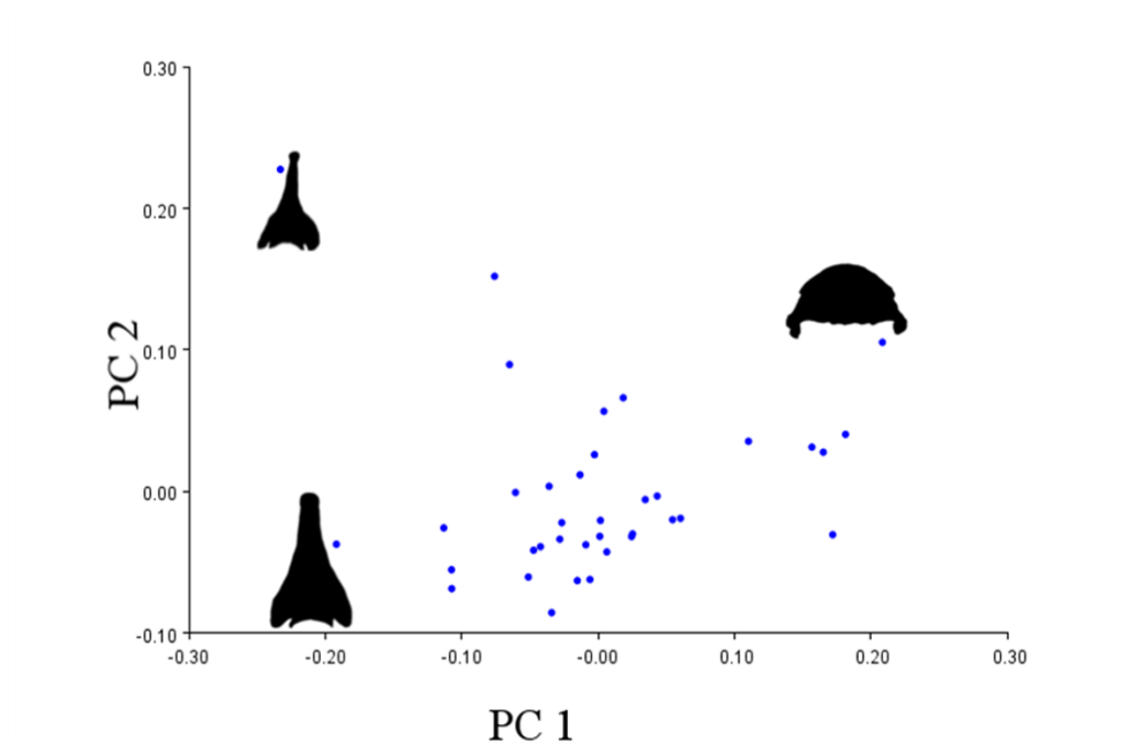


Figure 4.7 Position in morphospace of 36 stereospondyl species, along PC1 and PC2 based on 31 discrete landmarks on the palate. Skull shapes of *Platyoposaurus stuckenbergi* (top left), *Australerpeton cosgriffi* (bottom left) and *Vigilius wellesi* (right) are illustrated to show the relative skull shapes at PC extremes. The fully labelled plot is electronic appendix EA3.

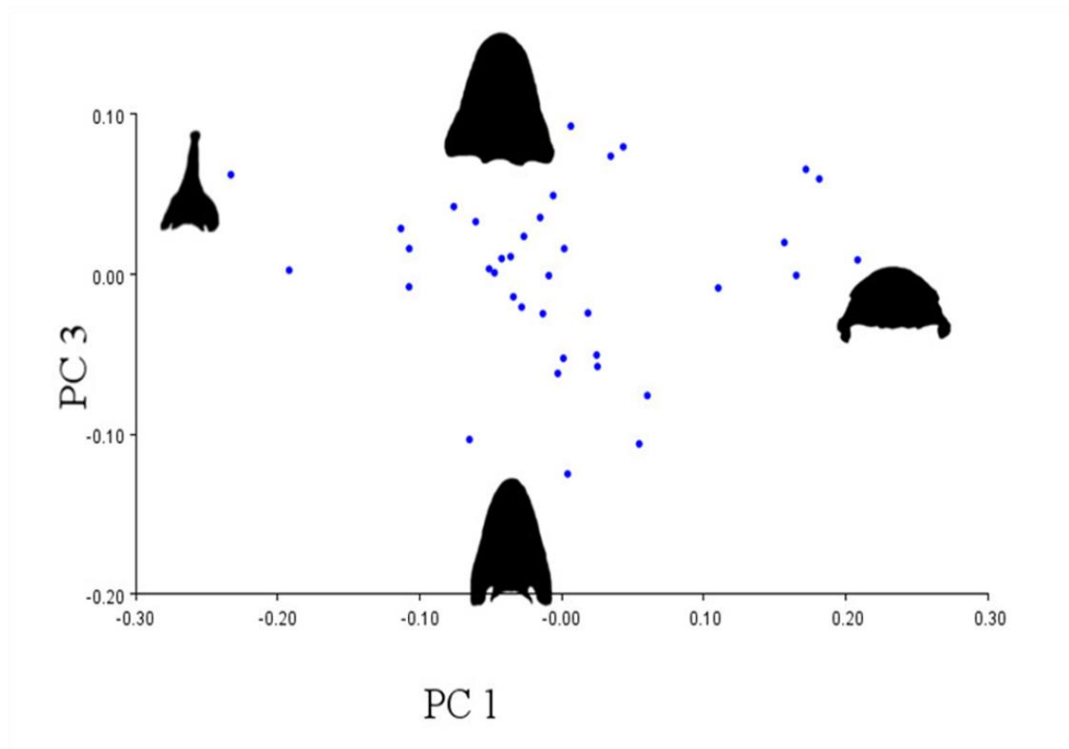


Figure 4.8 Position in morphospace of 36 stereospondyl species, along PC1 and PC3 based on 31 discrete landmarks on the palate. *Platyoposaurus stuckenbergi* (left), *Vigilius wellesi* (right) and *Anaschisma browni* (top centre) and *Rhineceps nyaensis* (bottom centre) are illustrated. The fully labelled plot is electronic appendix EA3.

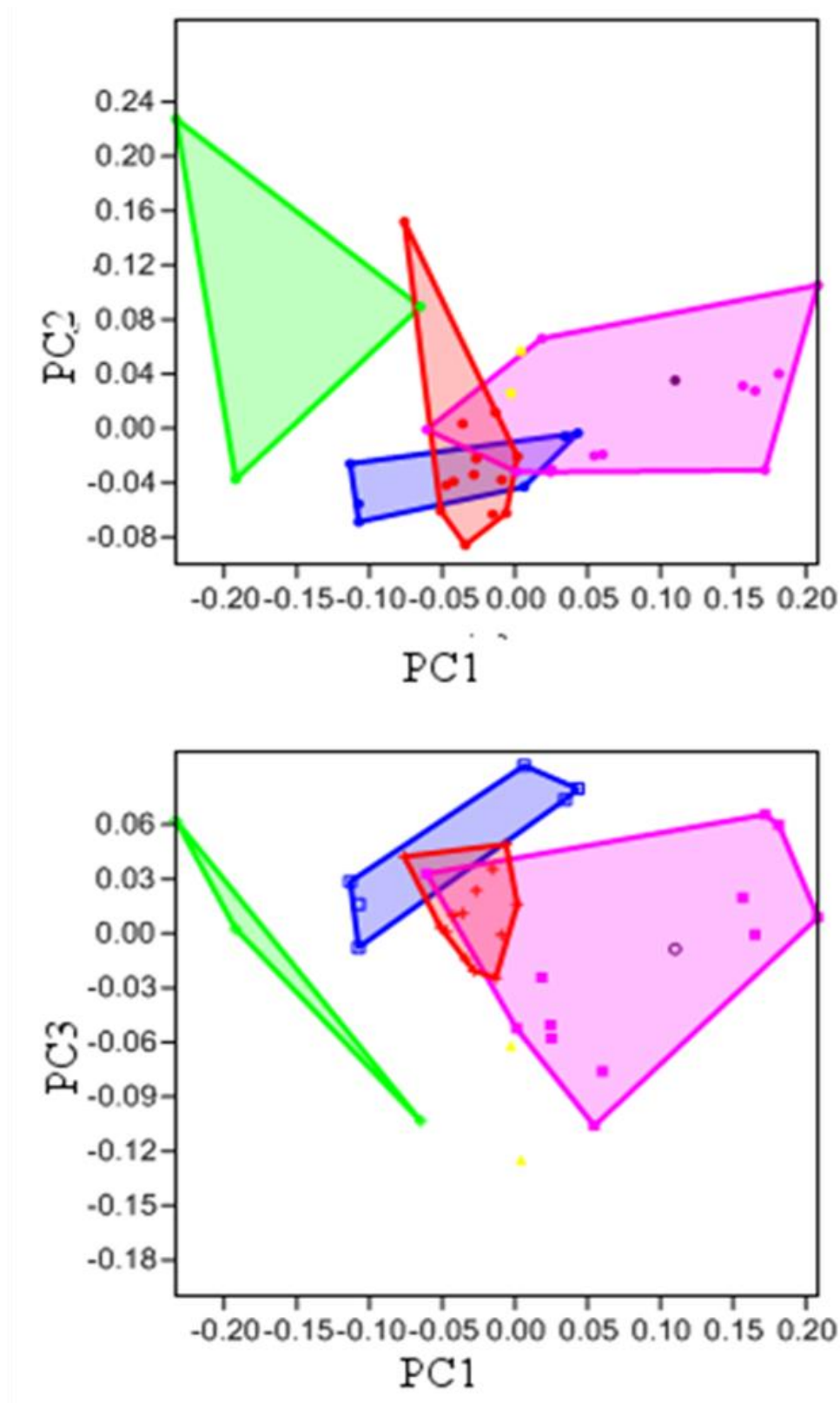


Figure 4.9 Position in morphospace of 36 stereospondyl species, along PC1 and PC2 (above) and PC1 and PC3 (below), based on 31 discrete palatal landmarks. Convex hulls delimit taxa according to their taxonomic group affiliation (as per Schoch and Milner, 2000): Archegosauridae - bright green, Trematosauroidae - blue, Rhinesuchidae-yellow, Brachyopoidea - purple, Rhytidosteoidea - pink, Capitosauroidae - red.

Table 4.5 Pairwise comparisons of PC1 and PC2 scores of palate discreet landmarks, designated by taxonomic group. PERMANOVA values are above the diagonal and ANOSIM values are below the diagonal. Bonferonni sequential significant values are indicated in bold. Stem and Plagiosauridae excluded.

Abbreviations are as follows Stem = Stem stereospondyls, Arch = Archegosauridae, Brachy = Brachyopoidea, Plag = Plagiosauridae, Tremat = Trematosauroida, Rhine = Rhinesuchidae, Rhyt = Rhytidosteoidea, Capit = Capitosauroida

	Arch	Tremat	Rhine	Rhyt	Capit
Arch		0.0137	0.2008	0.0027	0.0048
Tremat	0.0279		0.2149	0.0109	0.8547
Rhine	0.3037	0.2105		0.2169	0.124
Rhyt	0.0027	0.0702	0.5027		0.0001
Capit	0.0055	0.0067	0.0557	0.0001	

	Arch	Tremat	Rhine	Rhyt	Capit
Arch		0.0238	0.1947	0.0023	0.0076
Tremat	0.0113		0.0378	0.0035	0.33
Rhine	0.2972	0.0336		0.1421	0.0209
Rhyt	0.0023	0.0177	0.379		0.0001
Capit	0.0049	0.0007	0.0301	0.0001	

4.3.3 Skull outlines using semilandmarks

Almost all of the variation in the skull outlines of stereospondyls was explained by the first two principal components (Figure 4.10). The first PC accounted for 70% of the variance whereas PC2 accounted for ~10%. Variation in PC1 reflected the length and narrowness of the skull, which was not restricted to the anterior part of the skull, but the entire length of the skull, indicating that this applied to more than just the rostrum (Figure 4.10). The long and narrow *Aphaneramma rostratum* occupied the most positive position, and the wide headed *Gerrothorax pulcherrimus* had the most negative value (Figure

4.11). A plot of PC1 and PC2 showed the variation on the PC1 axis was greater compared to PC2, Levene's test showed this was significant ($F = 48.366$, $P < 0.0001$, Figure 4.11). This, combined with the high percentage variance suggests that the elongation of the skull was an important variant of the overall skull outline. Variation in PC2 showed a shift toward shorter snouts and wider posterior skull margins (Figure 4.10), a shape approaching an equilateral triangle, with *Quasicyclotosaurus campi* at the positive extreme and *Uralosuchus senekalensis* at the negative (Figure 4.11). *Uralosuchus* had substantial posterolateral projections beyond the posterior skull margin at the post-parietals.

PERMANOVA ($F = 18.42$, $P = 0.0001$) and ANOSIM ($R = 0.3735$, $P = 0.001$) both showed that there were significant differences across taxonomic group. Taxonomic group occupation of morphospace still had large ranges, but with more separation between convex hulls than observed for Epoch and continent (Figure 4.12). The Capitosauroidae and Trematosauroidae had large overlapping ranges and do not differ in the PERMANOVA results, but ANOSIM pairwise comparisons show the long and wide skulls of the Capitosauroidae were different from all other groups except for Archegosauridae which match them in skull length and the Rhinesuchidae, which match them in width. There were also no differences between Rhytidosteoidea and Brachyopoidea, both had wide posterior skull margins and short prenasal regions. There was no difference between the wide-headed Brachyopoidea and Plagiosauroidae (both represented by very low numbers of species), finally there was no difference between the Trematosauroidae and the Archegosauridae, both have a large variation in skull shapes, from long and triangular, to blunt snouted and short (see Discussion).

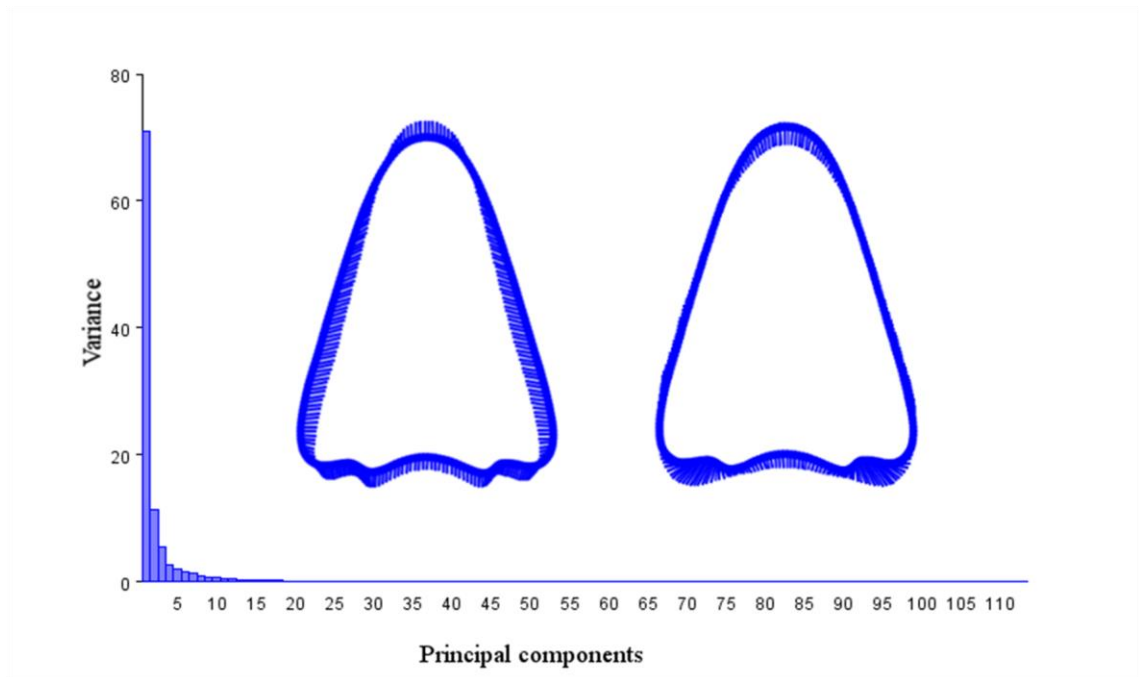


Figure 4.10 Variance explained by the Principal components of 250 semilandmarks around the skull roof of 114 stereospondyls. Scree plots of PC1 (left) and PC2 (right) are shown. The anterior of the skull roof is toward the top of the page.

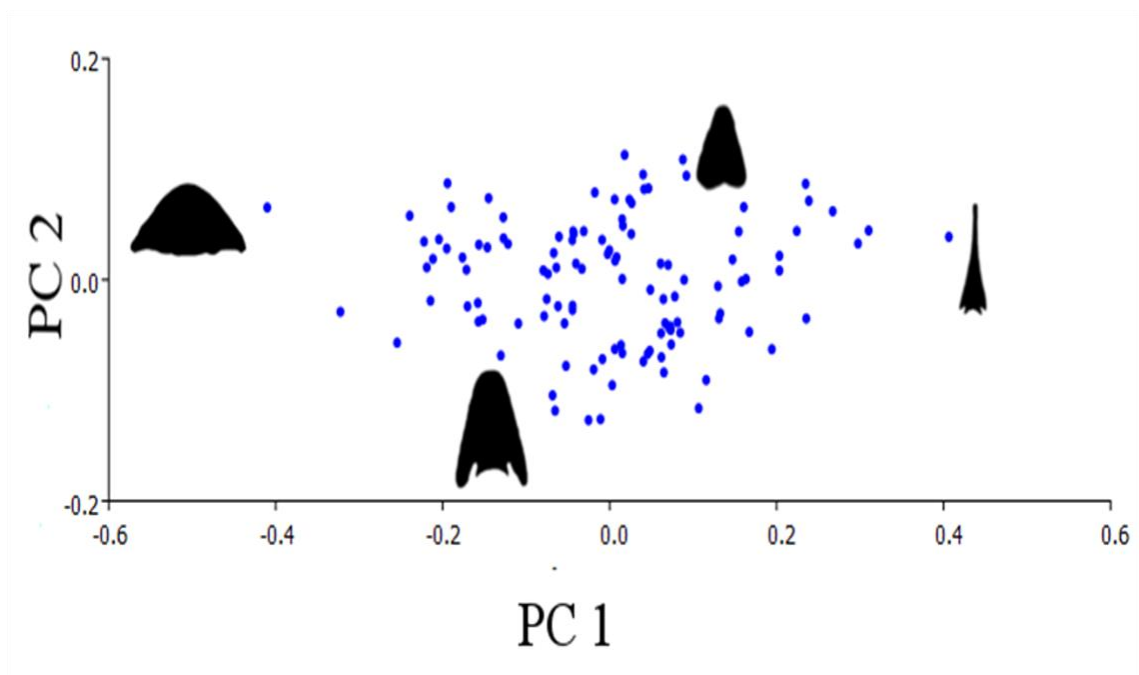


Figure 4.11 Position in morphospace of the skull shape of 114 stereospondyl species, along PC1 and PC2, based on 250 evenly spaced semilandmarks. *Gerrothorax pulcherrimus* and *Aphaneramma rostratum* illustrate the negative and positive extremes of PC1, *Uralosuchus senekalensis* and *Quasicyclotosaurus campi* illustrate the negative and positive extremes of PC2. Fully labelled plots are in electronic appendix EA.3.

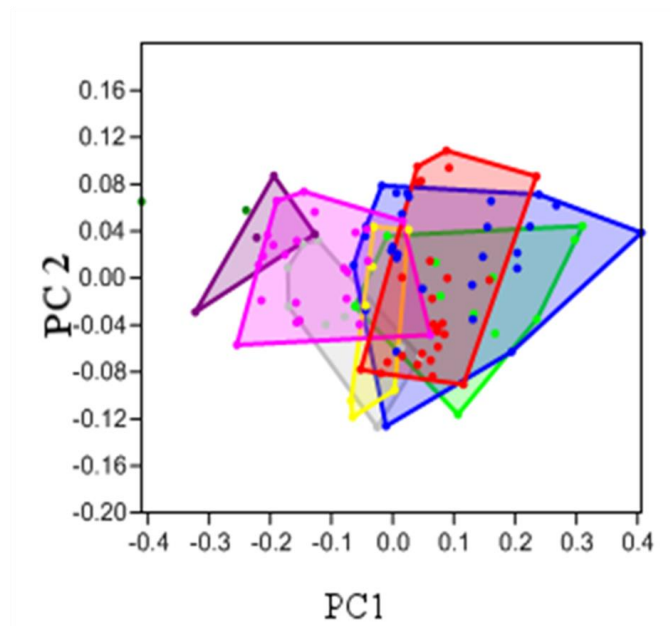


Figure 4.12 Position in morphospace of the skull shape of 114 stereospondyl species, along PC1 and PC2, based on 250 evenly spaced semilandmarks, with convex hulls delimiting taxa as categorised according to their taxonomic group affiliation; Archegosauridae - bright green, Trematosauroidae - blue, Rhinesuchidae-yellow, Stem stereospondyl - grey, Brachyopoidea - purple, Rhytidosteoidea - pink, Capitosauroidae - red, Plagiosauridae - dark green

Table 4.6 Pairwise comparisons of PC1 and PC2 scores of skull outline semilandmarks, designated by taxonomic group. PERMANOVA values are above the diagonal and ANOSIM values are below the diagonal. Sequential Bonferroni corrected significant values are indicated in bold.

Abbreviations are as follows Stem = Stem stereospondyls, Arch = Archegosauridae, Brachy = Brachyopoidea, Plag = Plagiosauridae, Tremat = Trematosauroidae, Rhine = Rhinesuchidae, Rhyt = Rhytidosteoidea, Capit = Capitosauroidae

	Stem	Arch	Plag	Brachy	Tremat	Rhine	Rhyt	Capit
Stem		0.0003	0.0182	0.0146	0.0002	0.2341	0.0898	0.0001
Arch	0.0006		0.0104	0.0011	0.1835	0.0033	0.0001	0.0217
Plag	0.0195	0.0127		0.2631	0.0022	0.0289	0.0061	0.0023
Brachy	0.0619	0.0009	0.2674		0.0001	0.0003	0.0547	0.0001
Tremat	0.004	0.2114	0.0023	0.0002		0.0087	0.0001	0.1303
Rhine	0.1135	0.0076	0.0275	0.0021	0.2469		0.0038	0.003
Rhyt	0.2305	0.0001	0.0166	0.2039	0.0001	0.001		0.0001
Capit	0.0001	0.0073	0.0027	0.0001	0.0028	0.014	0.0001	

4.3.4 Orbit shape using semilandmarks

The first two principal components accounted for 80% of the variation in orbit outlines (Figure 4.13). There was no significant difference in the variance of distribution of species along the axes (Levene's test, $F = 2.623$, $P = 0.107$). A plot of PC1 and PC2 showed that the resulting morphospace occupation of the 119 taxa represented here showed no discernible clustering or patterns (Figure 4.14). Variation in PC1 represented changes in the length and narrowness of the orbit (Figure 4.13). At its most positive end is *Plagiosuchus pustuliferous* (Plagiosauridae), which had a very unusual orbit, it was neither ovoid nor round, but almost rectangular, and twice as long as it is wide. *Sclerocephalus frossardi* (Archegosauridae), with a circular orbit, is at the most negative position (illustrated on Figure 4.14). By contrast, variation in PC2 showed an anteromedial expansion with a corresponding posterolateral movement (Figure 4.13). This seems to be indicative of a change in orientation of the orbit as seen in *Limnokoites paludinitans* (Rhytidosteoidea), at the opposing end of PC2 was the anteriorly-posteriorly orientated oval orbit of *Archegosaurus dyscriton* from the Archegosauridae (shown in Figure 4.14).

There was a significant difference between the orbits when they were affiliated with their taxonomic group (PERMANOVA $F = 1.783$, $P = 0.0429$, ANOSIM $R = 0.09663$, $P = 0.0024$). There were overlaps for all of the taxonomic groups, but several of them had outliers in a particular direction (Figure 4.15). Brachyopoidea, had several taxa in the most positive positions on PC2, suggestive of orbits along a diagonal axis (Figure 4.14), and were significantly different from all other taxonomic groups except for the Plagiosauridae (Table 4.7). Both of these groups had only two and three taxa, respectively. The R value was very low (< 0.1), so the model is not strongly supported. ANOSIM and PERMANOVA both showed there was a significant difference between the Capitosauroida and Brachyopoidea, the former had very round orbits aligned with the midline of the skull (Table 4.7).

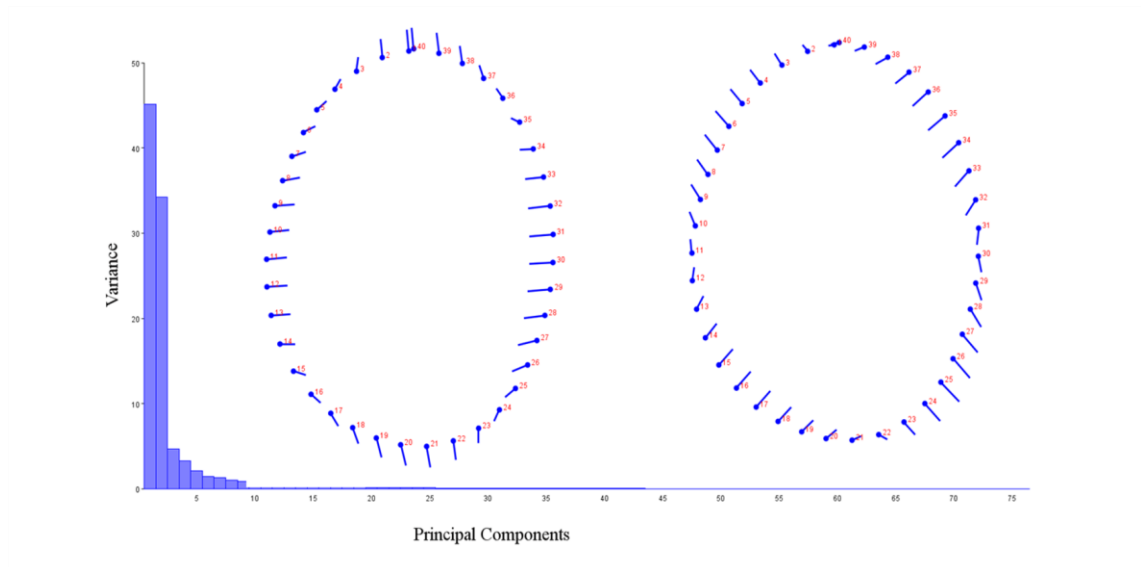


Figure 4.13 Variance explained by the Principal components of 40 semilandmarks around the orbit of 119 stereospondyls. Scree plots of PC1 (left) and PC2 (right) are shown. The anterior of the orbit is toward the top of the page.

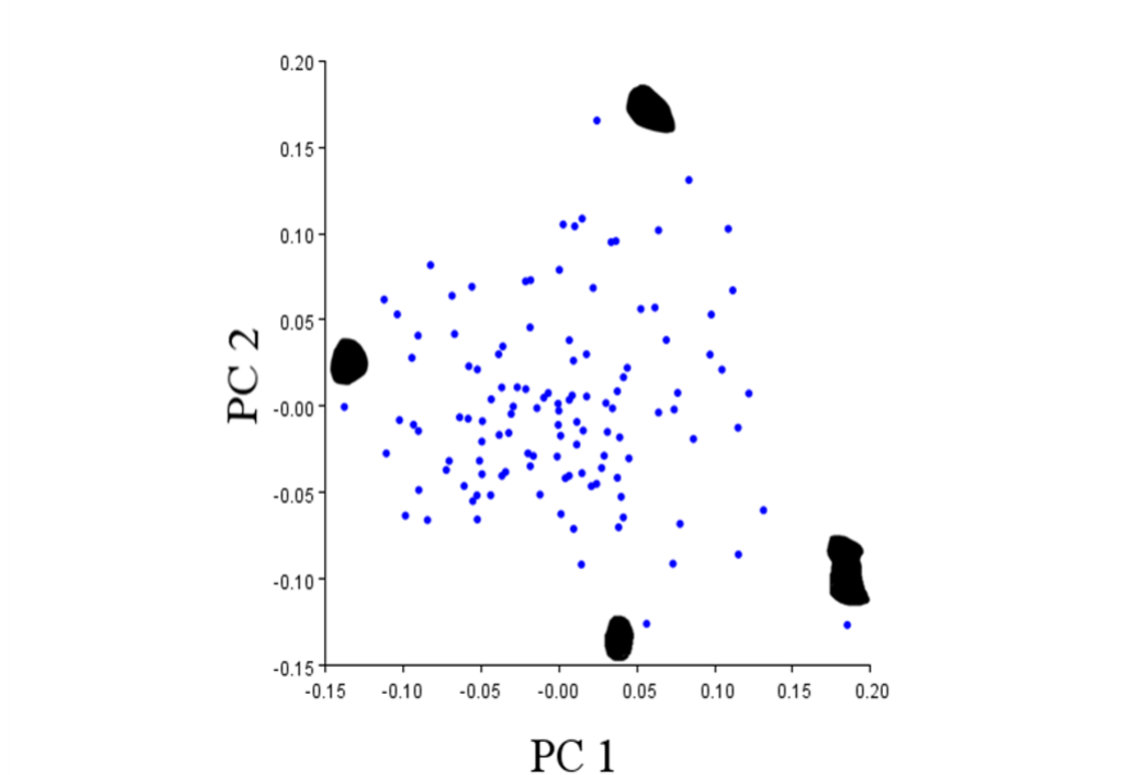


Figure 4.14 Position in morphospace of orbital shape of 119 stereospondyl species, along PC1 and PC2, based on 40 evenly spaced semilandmarks. The orbit silhouette of *Plagiosuchus pustuliferous* and *Sclerocephalus frossardi* illustrate the positive and negative extremes of PC1. *Limnokoites paludinitans* and *Archegosaurus dyscriton* illustrate the positive and negative extremes of PC2. The fully labelled plot is in electronic appendix EA 3.

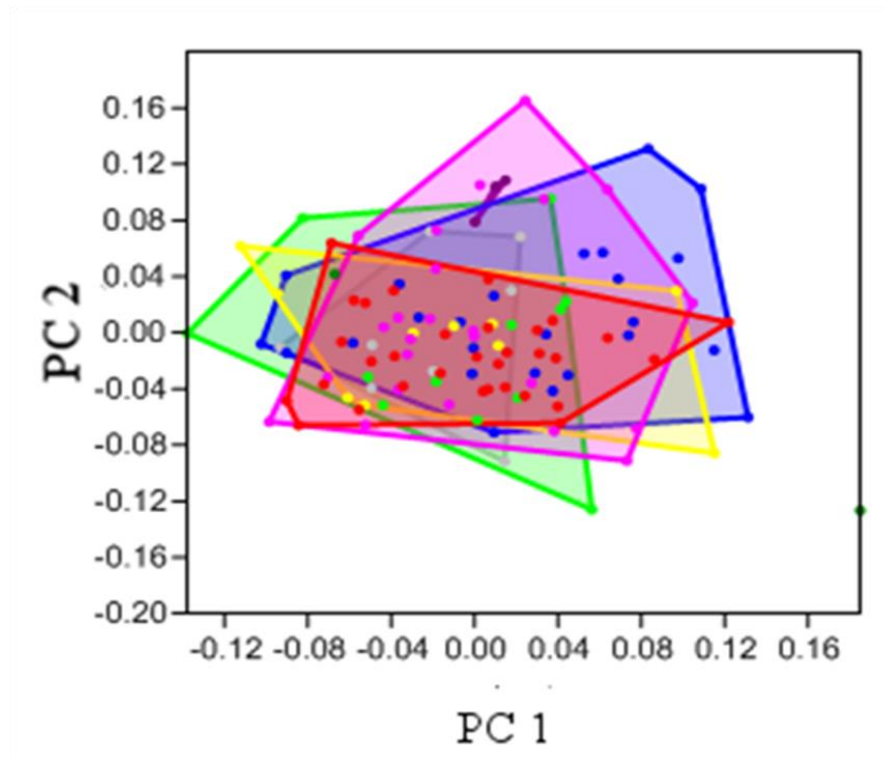


Figure 4.15 Position in morphospace of orbital shape of 119 stereospondyl species, along PC1 and PC2, based on 40 evenly spaced semilandmarks. The convex hull delimit taxa according to their taxonomic group affiliation (as per Schoch and Milner, 2000); Archegosauridae - bright green, Trematosauroidae – blue, Rhinesuchidae-yellow, Stem stereospondyl – grey, Brachyopoidea – purple, Rhytidosteoidea – pink, Capitosauroidae – red, Plagiosauridae – dark green (single point).

Table 4.7 Pairwise comparisons of PC1 and PC2 scores of orbit outline semilandmarks, designated by taxonomic group. NPMANOVA values are above the diagonal and ANOSIM values are below the diagonal. Significant values are indicated in bold.

Abbreviations are as follows Stem = Stem stereospondyls, Arch = Archegosauridae, Brachy = Brachyopoidea, Plag = Plagiosauridae, Tremat = Trematosauroidae, Rhine = Rhinesuchidae, Rhyt = Rhytidosteoidea, Capit = Capitosauroidae

	Stem	Arch	Plag	Brachy	Tremat	Rhine	Rhyt	Capit
Stem		0.8293	0.274	0.0178	0.1097	0.9206	0.6841	0.3968
arch	0.9254		0.3635	0.0096	0.1559	0.9765	0.6759	0.909
Plag	0.1318	0.0671		0.2025	0.3973	0.3523	0.2389	0.1555
Brachy	0.0529	0.0952	0.0988		0.0369	0.0257	0.04	0.0006
Tremat	0.3721	0.2924	0.031	0.1046		0.1809	0.2436	0.0164
Rhine	0.9043	0.8957	0.1367	0.0721	0.3084		0.7867	0.7399
Rhyt	0.8766	0.5922	0.0607	0.2655	0.1262	0.5706		0.2403
Capit	0.1207	0.0638	0.0101	0.0005	0.0082	0.0962	0.0244	

4.3.5 Naris shape using semilandmarks

As with the orbital outline, the first two principal components of naris outlines accounted for 80% of the variation (Figure 4.16). Increasingly positive values of PC1 were associated with an overall lengthening and narrowing in the naris. This was illustrated by the long snouted *Cosgriffus campi* (Trematosauroidae) at the positive end of PC1, and the rounded naris of *Sclerocephalus frossardi* at the opposite end (Figures 4.16 and 4.17). Variation in PC2 had an anteromedial expansion with a corresponding posterolateral movement with increasingly positive values. This seemed to be indicative of a change in orientation of the naris as seen in *Limnokoites paludinitans* (Rhytidosteoidea), which again occupied the most positive position on PC2. By contrast, *Aphaneramma rostratum* (Trematosauroidae) had a long but comparably wide naris at the negative end of PC2 (Figure 4.17). A plot of PC1 and PC2 created a distribution of taxa in morphospace that had a central cluster, though not a close one, and Levene's test showed that there was a significant difference between the variance of taxa distribution along the two PCs ($F = 16.073$, $p < 0.0001$).

PERMANOVA ($F = 2.424$, $P = 0.0143$) and ANOSIM ($R = 0.1261$, $P = 0.0005$) results showed that there were significant differences between the naris shapes of different taxonomic groups (Table 4.8, Figure 4.8). The ANOSIM showed that Rhytidosteoidea and Archegosauridae were significantly different, the former occupied more positive positions on PC2 with nares that were aligned with the skull margin rather than the midline (Table 4.8, Figure 4.8). Capitosauroidae were significantly different from Archegosauridae (ANOSIM only), stem stereospondyls (PERMANOVA only) and Brachyopoidea (both) (Table 4.8), which was unexpected as they occupied the most central position in morphospace, overlapped by the convex hulls of all other taxonomic groups (Figure 4.18). However, they had a large number of taxa in a small area, which supported the ANOSIM model output. Again we had low R values for the ANOSIM, suggesting that these data were not well explained by the model (< 0.15).

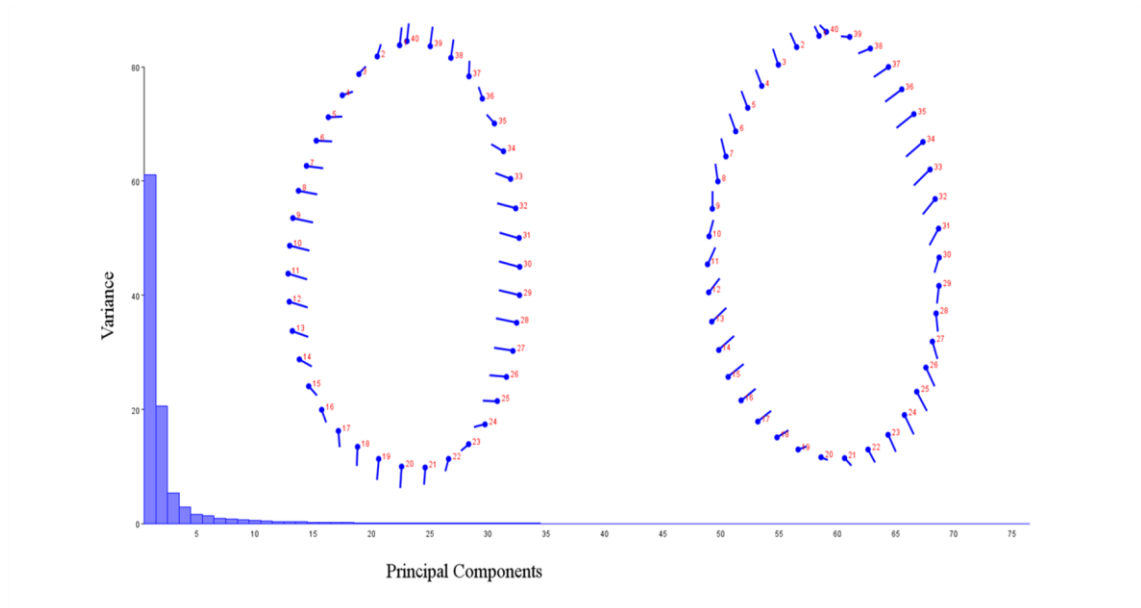


Figure 4.16 Variance explained by the Principal components of 40 semilandmarks around the naris of 95 stereospondyls, plots of PC1 (left) and PC2 (right) are shown. The anterior of the naris is toward the top of the page.

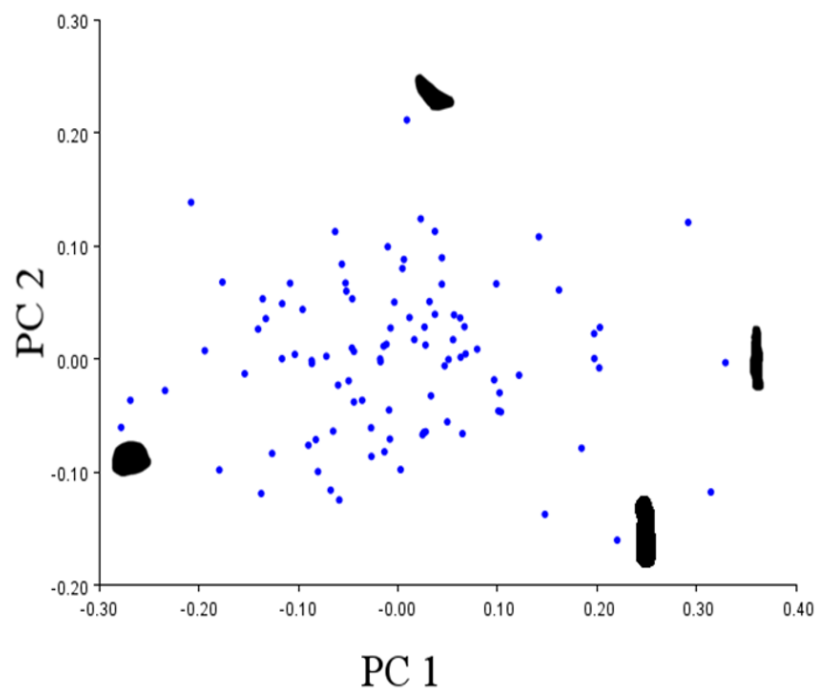


Figure 4.17 Position in morphospace of naris shape of 95 stereospondyl species, along PC1 and PC2, based on 40 evenly spaced semilandmarks. Naris silhouettes of *Cosgriffus campi* (right) and *Sclerocephalus frossardi* represent the most positive and negative positions on PC1. *Limnokoites paludinitans* and *Aphaneramma rostratum* illustrate the most positive and negative positions on PC2. A fully labelled plot is in electronic appendix EA 3.

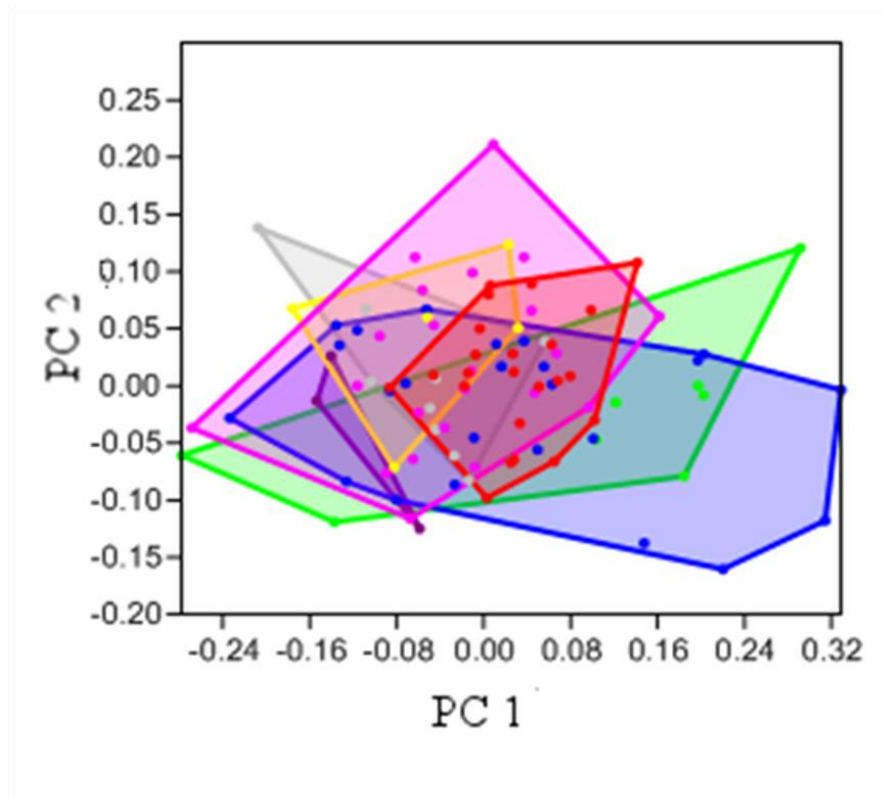


Figure 4.18 Position in morphospace of naris shape of 95 stereospondyl species, along PC1 and PC2, based on 40 evenly spaced semilandmarks. Convex hulls delimit taxa as categorised according to their taxonomic group affiliation (as per Schoch and Milner 2000); Archegosauridae - bright green, Trematosauroidae - blue, Rhinesuchidae-yellow, Stem stereospondyl - grey, Brachyopoidea - purple, Rhytidosteoidea - pink, Capitosauroidae - red, Plagiosauridae - dark green (single point).

Table 4.8 Pairwise comparisons of PC1 and PC2 scores of naris outline semilandmarks, designated by taxonomic group. NPMANOVA values are above the diagonal and ANOSIM values are below the diagonal. Bonferroni sequential corrected significant values are indicated in bold. Plagiosauridae are absent. Abbreviations are as follows Stem = Stem stereospondyls, Arch = Archegosauridae, Brachy = Brachyopoidea, Plag = Plagiosauridae, Tremat = Trematosauroidae, Rhine = Rhinesuchidae, Rhyt = Rhytidosteoidea, Capit = Capitosauroidae

	stem	Arch	Brachy	Tremat	Rhine	Rhyt	Capit
stem		0.0474	0.3335	0.0996	0.6242	0.4986	0.0008
Arch	0.003		0.1161	0.4911	0.1242	0.0263	0.1677
Brachy	0.3162	0.0911		0.1202	0.1977	0.1142	0.0008
Tremat	0.894	0.1104	0.4734		0.1648	0.0921	0.4496
Rhine	0.2325	0.039	0.3089	0.6485		0.6432	0.0111
Rhyt	0.7336	0.0002	0.2153	0.2831	0.5827		0.0293
Capit	0.0053	0.0001	0.0005	0.0051	0.0171	0.0115	

4.3.6 Lacrimal shape using semilandmarks

The lacrimal showed considerable plasticity in shape between the various stereospondyls (see Figure 4.1). The first two principal components accounted for over 85% of the variation nearly equally split between PC1 (40%) and PC2 (37%) (Figure 4.19). Levene's test showed no significant difference between the distribution of taxa along the axes ($F = 0.109$, $p = 0.742$).

The morphospace created by a plot of PC1 and PC2 showed a cluster in the mid-range of PC2 and the positive range of PC1, with several outliers on the positive of PC2 and negative of PC1 (Figure 4.20). PC1 showed variation which was associated with a long, narrow shape for extreme positive values (e.g. *Australerpeton cosgriffi*) and a more triangular shape for the extreme negative values (e.g. *Bothriceps australis*; Figure 4.20). Variation for PC2 showed an expansion in the anteromedial and posterolateral directions with the centre of the medial margin moving in an anterior direction and the centre of the lateral margin moving in a posterior direction when moving in the positive direction (Figure 4.20). At the positive end of the axis on PC2 is *Plagiosuchus pustuliferous* (Plagiosauridae), the lacrimal of which showed a change in orientation, when compared with the lacrimal of *Metoposaurus diagnosticus krajowensis* (Trematosauroidae) at the opposite end of the scale (Figure 4.20).

There were significant differences in the lacrimal between different taxonomic groups (PERMANOVA $F = 4.272$, $P = 0.0001$, ANOSIM $R = 0.2328$, $P = 0.0001$). It appeared as though the convex hull of the Trematosauroidae coincided with the Capitosauroidae, but only three taxa from that group fell within the range of the Capitosauroidae (Figure 4.21). The pairwise comparisons of both tests concur (Table 4.9). ANOSIM showed Capitosauroidae differed from Archegosauridae and Brachyopoidea, as the Capitosauroidae fell in between the other two taxonomic groups on PC1. The Brachyopoidea, with their foreshortened skull tables, had lacrimals that were as wide as they were long, whereas the Archegosauridae had mostly long and narrow lacrimals. The Capitosauroidae had more species with lacrimals that were orientated with the skull midline rather than the margin. The difference between Brachyopoidea and Capitosauroidae was not supported by the PERMANOVA when sequential correction is applied. The PERMANOVA identified an additional difference between Capitosauroidae and stem stereospondyls, where the latter had diagonally orientated lacrimals.

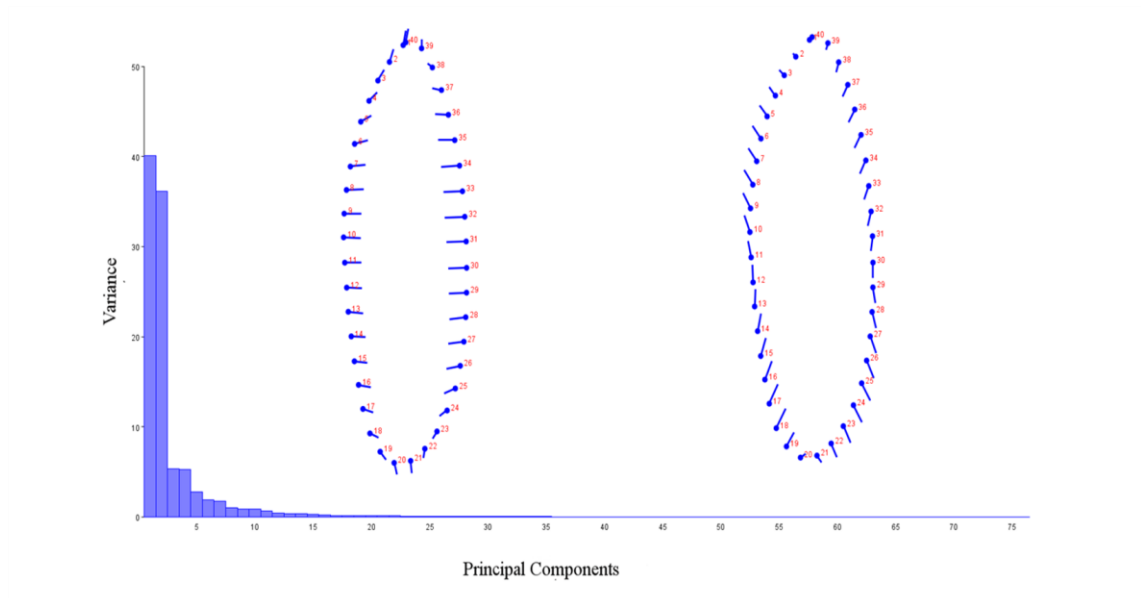


Figure 4.19 Variance explained by the Principal components of 40 semilandmarks around the lacrimal of 77 stereospondyls. Scree plots of PC1 (left) and PC2 (right) are shown. The anterior margin of the lacrimal is toward the top of the page.

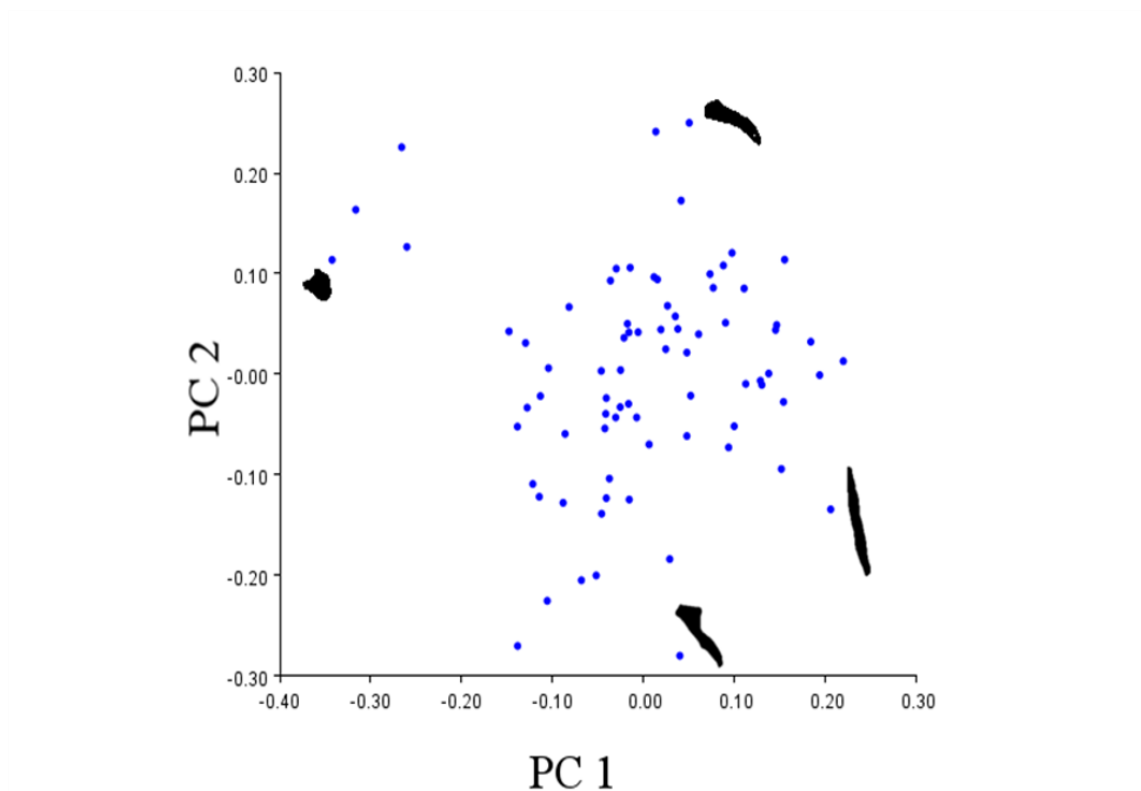


Figure 4.20 Position in morphospace of lacrimal shape of 77 stereospondyl species, along PC1 and PC2 based on 40 evenly spaced semilandmarks. *Australerpeton cosgriffi* and *Bothriceps australis* lacrimal silhouettes illustrate the positive and negative extremes of PC1. *Plagiosaurus pustuliferous* and *Metoposaurus diagnosticus krasjowiensis* illustrate the positive and negative extremes of PC2. A fully labelled plot is in electronic appendix EA 3.

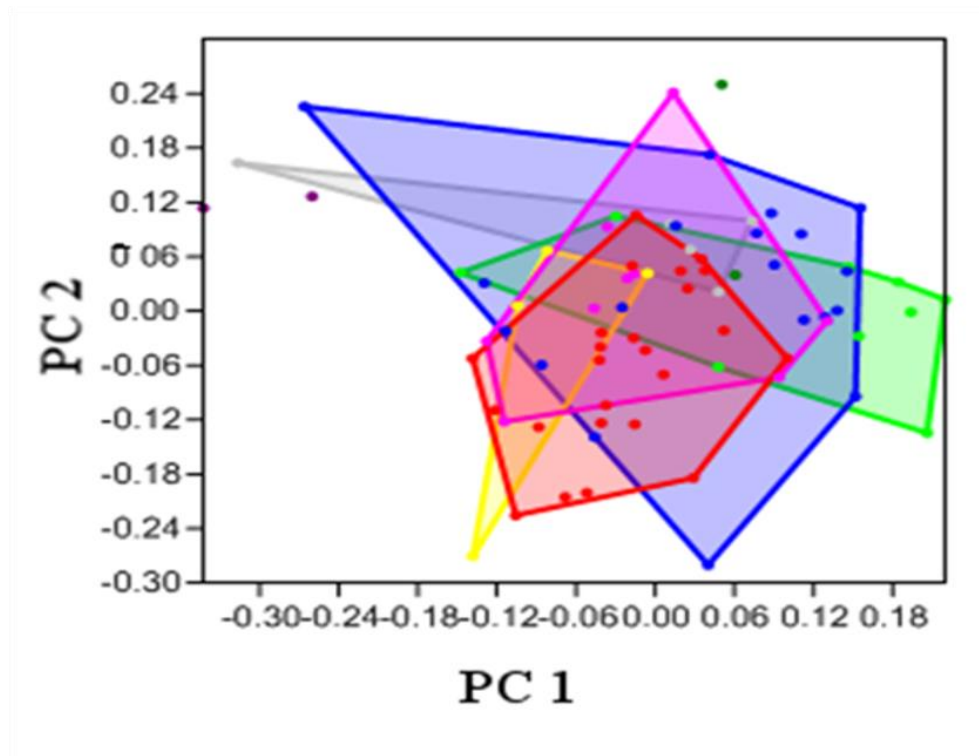


Figure 4.21 Position in morphospace of lacrimal shapes of 77 stereospondyl species, along PC1 and PC2, based on 40 evenly spaced semilandmarks. Convex hulls delimit taxa according to their taxonomic group affiliation as per Scoch and Milner, 2000); Archegosauridae - bright green, Trematosauroidae – blue, Rhinesuchidae - yellow, Stem stereospondyl – grey, Brachyopoidea – purple, Rhytidosteoidea – pink, Capitosauroidae – red, Plagiosauridae – dark green (single point)

Table 4.9 Pairwise comparisons of PC1 and PC2 scores of lacrimal outline semilandmarks, designated by taxonomic group. NPMANOVA values are above the diagonal and ANOSIM values are below the diagonal. Bonferroni sequentially corrected significant values are indicated in bold.

Abbreviations are as follows Stem = Stem stereospondyls, Arch = Archegosauridae, Brachy = Brachyopoidea, Plag = Plagiosauridae, Tremat = Trematosauroidae, Rhine = Rhinesuchidae, Rhyt = Rhytidosteoidea, Capit = Capitosauroidae

	Stem	Arch	Plag	Brachy	Tremat	Rhine	Rhyt	Capit
Stem		0.0547	0.6168	0.0966	0.2796	0.2014	0.5139	0.0017
Arch	0.1017		0.1859	0.0183	0.2419	0.0325	0.0437	0.0004
Plag	0.5207	0.1707		0.3299	0.3039	0.1303	0.1608	0.0077
Brachy	0.1034	0.0172	0.3376		0.009	0.0633	0.0192	0.0041
Tremat	0.5989	0.4492	0.4118	0.0083		0.1408	0.5845	0.0041
Rhine	0.0923	0.0197	0.2623	0.2021	0.2406		0.3453	0.3395
Rhyt	0.3574	0.0395	0.2915	0.019	0.5412	0.5451		0.0578
Capit	0.0137	0.0001	0.0276	0.0034	0.0008	0.0581	0.0695	

4.3.7 Tabular shape using semilandmarks

PC1 accounted for 75% of the variation in the tabular, as taxa moved toward the positive position of PC1 they showed the anterolateral corner of the tabular moving in a posteromedial direction as the posterolateral corner moves in a posterolateral direction (Figure 4.22). There was also anterolateral movement from the posteromedial corner with movement along the positive direction of PC1 (Figure 4.22), *Wetlugasaurus angustifrons* (Trematosauroidae) represented the positive extent of this movement, with *Trematosaurus brauni* (Trematosauroidae) at the opposite end of the axis (Figure 4.23). PC2 accounted for 27% of the variance and showed a reduction in the anterior-posterior distance and an increase in the medial-lateral directions toward the positive extreme of this axis (Figure 4.22), this was exemplified by the long and thin tabular of *Rhineceps nyaensis* at the most positive position on PC2 (illustrated on Figure 4.36). Moving in the opposite direction, the tabular became wider and shorter, as in *Batrasuchoides lacer* (Figure 4.23).

The morphospace created by PC1 and PC2 had a wide spread of taxa that were relatively evenly distributed, without the typical “cluster and outlier” pattern of most morphospace (Figure 4.23). This suggested that there was a range of tabular shapes, with many interim shapes, not a series of types. Levene’s test showed that there was a significant difference between the variance of taxa distribution along the two PCs ($F = 16.073$, $P < 0.0001$).

Both PERMANOVA ($F = 2.442$, $P = 0.0032$) and ANOSIM ($R = 0.08$, $= 0.0033$) identified significant differences between the tabular outlines and showed the same pattern of pairwise differences (Table 4.10). The Brachyopoidea had taxa in the most negative position on PC2, excepting *Bothriceps australis* and *Broomulus dutoiti* (Figure 4.24), and were significantly different from the Capitosauroidae. The negative position on PC2 showed that these Brachyopoidea had tabulars that lacked any distinct horn-like projection. The Capitosauroidae had distinct horns but their orientation ranged between directly posterior and closing into an otic notch. It is worth noting that the R value for the ANOSIM was very low, so taxonomic group affiliation was a significant but poor explanation for the position in morphospace.

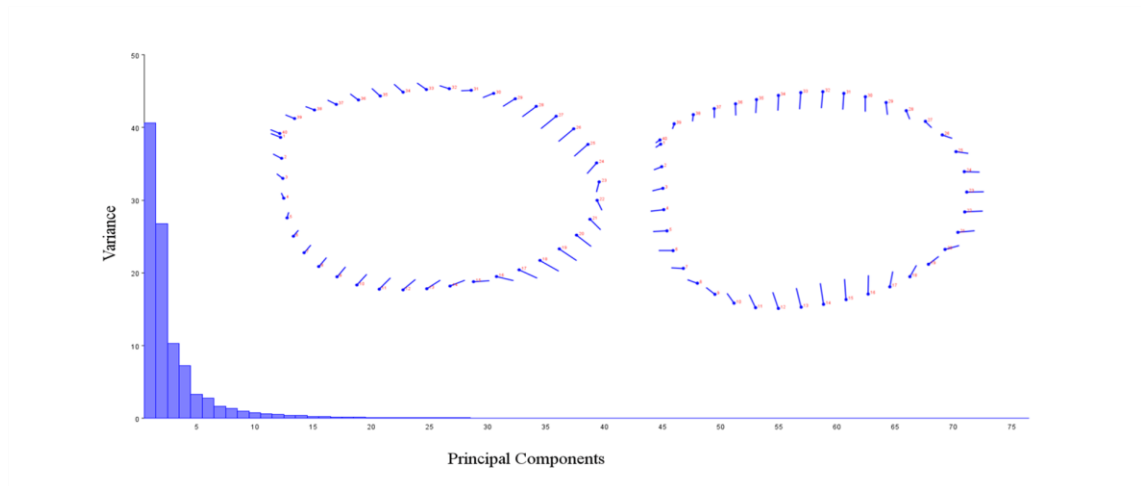


Figure 4.22 Variance explained by the Principal components of 40 semilandmarks around the tabular of 114 stereospondyls. Scree plots of PC1 (left) and PC2 (right) are shown, the anterior margin of the tabular is toward the top of the page.

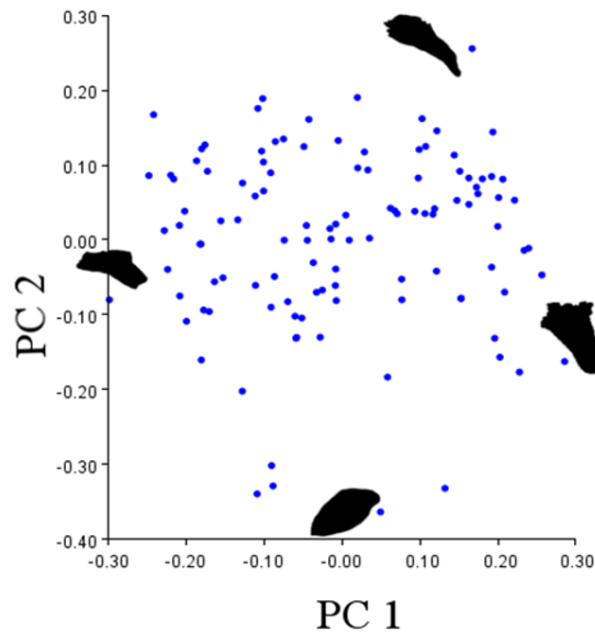


Figure 4.23 Position in morphospace of tabular shapes of 114 stereospondyl species, along PC1 and PC2 based on 40 evenly spaced semilandmarks. *Wetlugasaurus angustifrons* and *Trematosaurus brauni* tabular silhouettes illustrate the positive and negative extremes of PC1. *Rhineceps nyasaensis* and *Batrasuchoides lacer* illustrate the positive and negative extremes of PC2. A fully labelled plot is in electronic appendix EA 3.

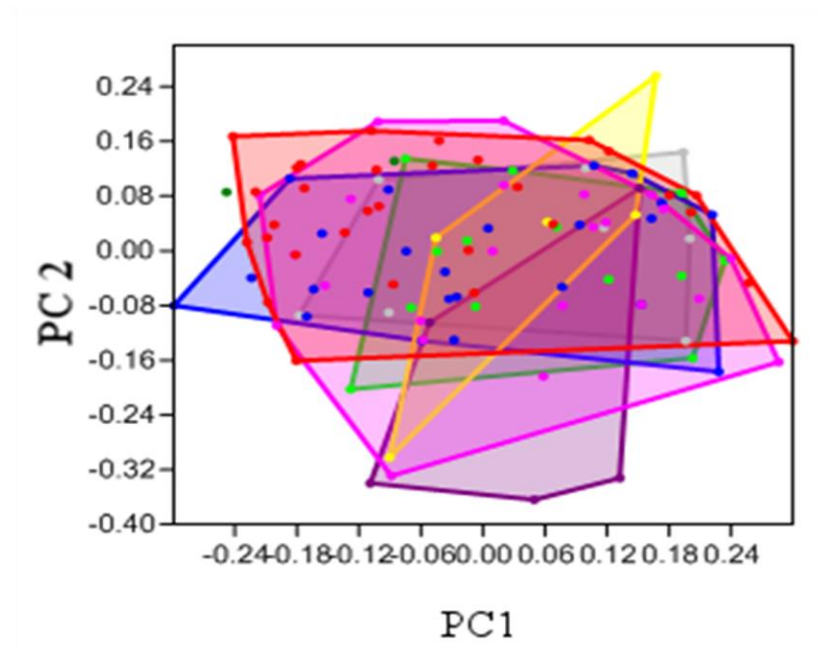


Figure 4.24 Position in morphospace of tabular shapes of 114 stereospondyl species, along PC1 and PC2, based on 40 evenly spaced semilandmarks. Convex hulls delimit taxa according to their taxonomic group affiliation (as per Schoch and Milner, 2000); Archegosauridae - bright green, Trematosauroidae – blue, Rhinesuchidae-yellow, Stem stereospondyl – grey, Brachyopoidea – purple, Rhytidosteoidea – pink, Capitosauroidae – red, Plagiosauridae – dark green

Table 4.10 Pairwise comparisons of PC1 and PC2 scores of tabular outline semilandmarks, designated by taxonomic group. NPMANOVA values are above the diagonal and ANOSIM values are below the diagonal. Bonferonni sequentially corrected significant values are indicated in bold.

Abbreviations are as follows Stem = Stem stereospondyls, Arch = Archegosauridae, Brachy = Brachyopoidea, Plag = Plagiosauridae, Tremat = Trematosauroidae, Rhine = Rhinesuchidae, Rhyt = Rhytidosteoidea, Capit = Capitosauroidae

	Stem	Arch	Plag	Brachy	Tremat	Rhine	Rhyt	Capit
Stem		0.8461	0.1099	0.0444	0.3396	0.9959	0.7426	0.1096
Arch	0.5691		0.0095	0.0237	0.2569	0.8938	0.7905	0.0191
Plag	0.194	0.0377		0.0451	0.1186	0.2882	0.0838	0.3588
Brachy	0.0465	0.0103	0.0477		0.0094	0.1699	0.0214	0.0004
Tremat	0.2963	0.5486	0.148	0.004		0.5549	0.6271	0.0867
Rhine	0.7642	0.31	0.2794	0.2079	0.1739		0.8567	0.2664
Rhyt	0.7684	0.9891	0.1932	0.0189	0.5649	0.4553		0.0294
Capit	0.088	0.0439	0.7206	0.0005	0.0409	0.0741	0.0175	

4.3.8 Ectopterygoid shape using semilandmarks

The principal component analysis of the ectopterygoid, resulted in the first two PCs accounting for 71% of the variation, with PC1 representing 50% of the variance (Figure 4.25). PC1 showed an overall lengthening and narrowing in the ectopterygoid (Figure 4.25), though the narrowing was more significant than the lengthening. PC2 represented 21% of the variation and showed an expansion in the anterolateral and posteromedial directions along the positive direction of the axis (Figure 4.25).

There was a bias in the distribution of points towards the positive end of PC1, with more taxa positioned at the positive end of PC1 (Figure 4.26). Levene's test showed that there was a significant difference between the variance of taxa distribution along the two PCs ($F = 13.886$, $P < 0.0001$). The long snouted *Australerpeton cosgriffi* (Archegosauridae) was at the most positive position, its ectopterygoid was long and thin, and the triangular-headed *Bothriceps australis* (Brachyopoidea), which had an ectopterygoid that was as wide as it was long, occupied the most negative position (illustrated on Figure 4.26). For PC2 there was a narrower distribution of points, with outliers on both ends (Figure 4.26). Two metoposaurs (of the Trematosauroidae), *Anaschisma browni* and *Koskinidon perfectus* occupied the most positive and negative positions respectively, the former having a shorter and posteriorly wider ectopterygoid (Figure 4.26). *Koskinidon* had a medial expansion and was a longer shape than *Anaschisma*.

PERMANOVA ($F = 2.943$, $P = 0.0035$) and ANOSIM ($R = 0.1085$, $P = 0.0151$) showed significant differences between taxonomic groups. Brachyopoidea formed a small convex hull in the morphospace at the extreme negative values of PC1 and PC2, with ectopterygoids that were short and wide (Figure 4.27). The taxonomic group pairwise comparisons showed differences between the Brachyopoidea and Trematosauroidae and Capitosauroidae (Table 4.11). The Trematosauroidae had ectopterygoids that were overall narrower than the Brachyopoidea but varied in their shape, hence the overall similarity with the Capitosauroidae.

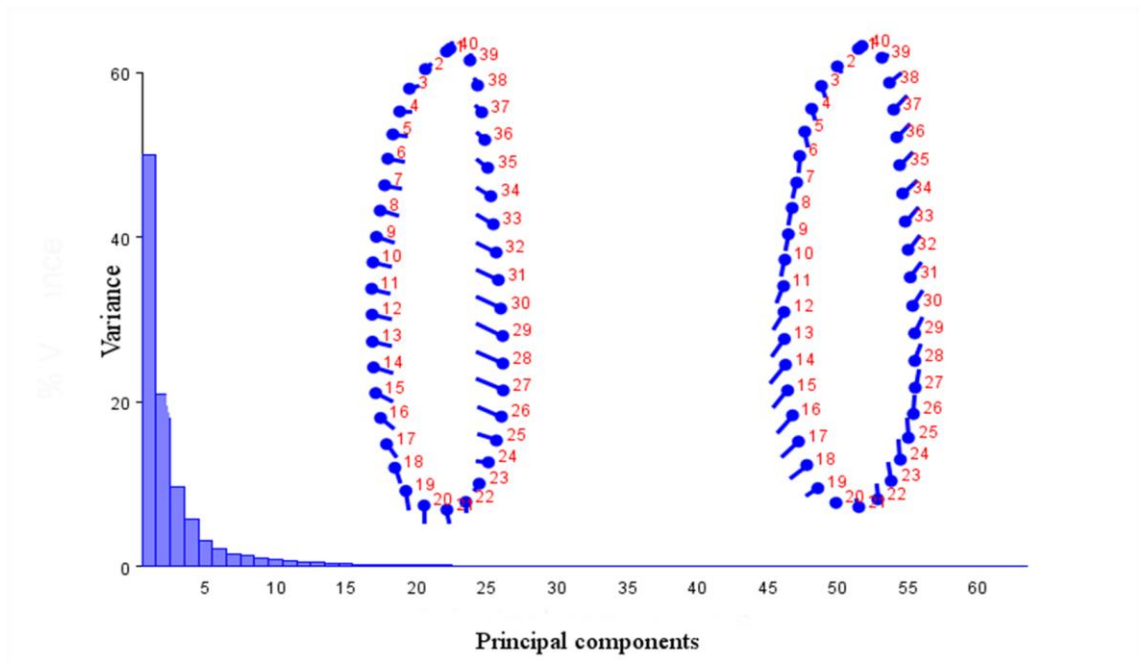


Figure 4.25 Variance explained by the Principal components of 40 semilandmarks around the ectopterygoid of 63 stereospondyl species. Scree plots of PC1 (left) and PC2 (right) are shown, the anterior of the ectopterygoid is toward the top of the page

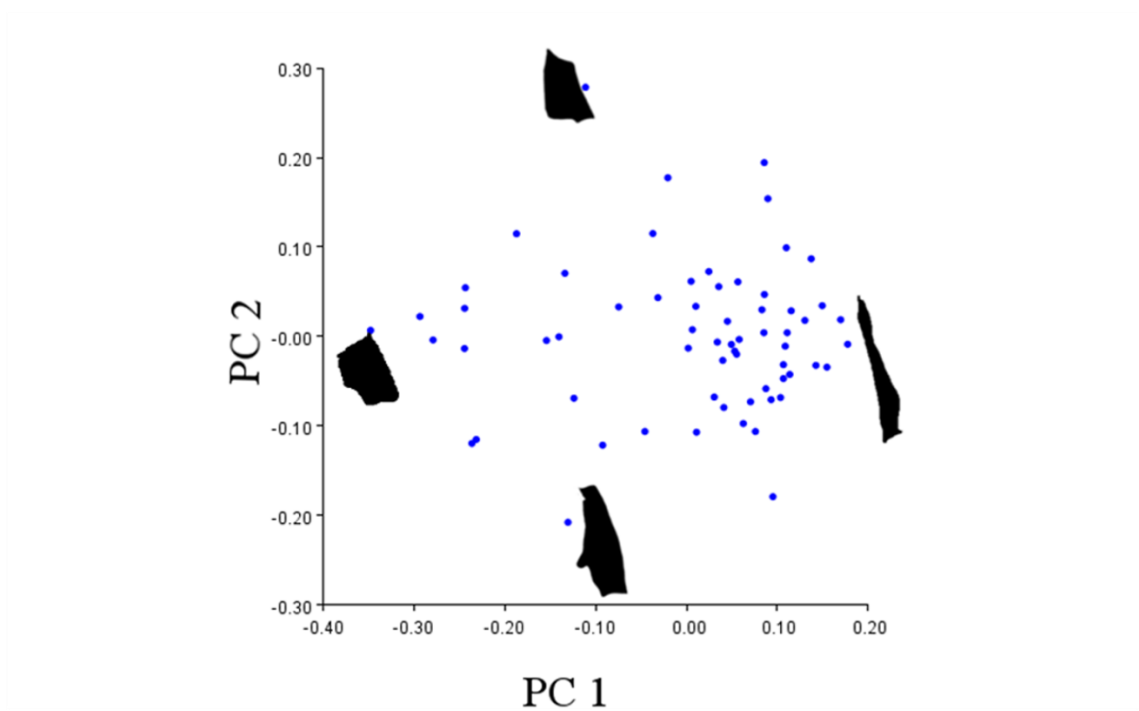


Figure 4.26 Position in morphospace of ectopterygoid shapes of 63 stereospondyl species, along PC1 and PC2, based on 40 evenly spaced semilandmarks. *Australerpeton cosgriffi* and *Bothriceps australis* ectopterygoid silhouettes illustrate the positive and negative extremes of PC1. *Anaschisma browni* and *Koskinodon perfectus* illustrate the positive and negative extremes of PC2. A fully labelled plot is in electronic appendix EA 3.

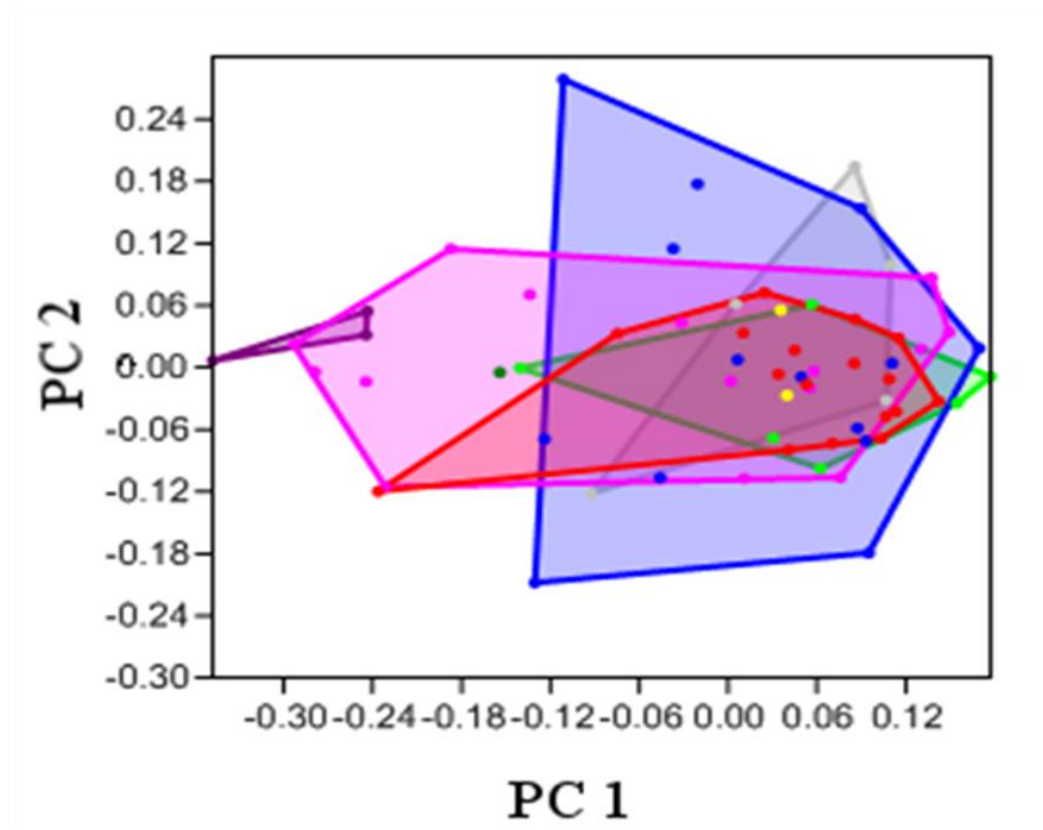


Figure 4.27 Position in morphospace of ectopterygoid shapes of 63 stereospondyl species, along PC1 and PC2, based on 40 evenly spaced semilandmarks. Convex hulls delimit taxa according to their taxonomic group affiliation (as per Schoch and Milner, 2000); Archegosauridae - bright green, Trematosauroidae - blue, Rhinesuchidae-yellow, Stem stereospondyl - grey, Brachyopoidea - purple, Rhytidosteoidea - pink, Capitosauroidae - red, Plagiosauridae - dark green (single point).

Table 4.11 Pairwise comparisons of PC1 and PC2 scores of ectopterygoid outline semilandmarks, designated by taxonomic group. NPMANOVA values are above the diagonal and ANOSIM values are below the diagonal. Bonferonni sequentially corrected significant values are indicated in bold.

Abbreviations are as follows Stem = Stem stereospondyls, Arch = Archegosauridae, Brachy = Brachyopoidea, Plag = Plagiosauridae, Tremat = Trematosauroidae, Rhine = Rhinesuchidae, Rhyt = Rhytidosteoidea, Capit = Capitosauroidae

	Stem	Arch	Brachy	Tremat	Rhine	Rhyt	Capit
Stem		0.5439	0.0184	0.7534	1	0.2552	0.4119
Arch	0.421		0.0125	0.6722	0.8187	0.1584	0.9456
Brachy	0.0171	0.0118		0.0021	0.0965	0.028	0.001
Tremat	0.8037	0.9006	0.0024		0.9576	0.3208	0.5902
Rhine	0.9515	0.8153	0.0994	0.9625		0.6034	0.8161
Rhyt	0.491	0.7807	0.0811	0.2896	0.9258		0.0354
Capit	0.05	0.1556	0.0008	0.0251	0.6588	0.0128	

4.3.9 Palatine shape using semilandmarks

PC1 accounted for 50% of the variance in palatine shape and toward the positive end of the axis there was posterior movement of the medial margin of the palatine as the lateral margin did the opposite, indicating a change in orientation along the positive direction of PC1 (Figure 4.28). PC2 accounted for 23% of the variation in palatine shape, the palatine became wider and shorter toward the positive direction, particularly in the anterior half (Figure 4.28).

When plotted there was no tight cluster of taxa on PC1 and the taxa appeared to have an even distribution along the axis (Figure 4.29). There was a significant difference in the variance of the taxa distribution on PC1 and PC2 (Levene's test, $F = 12.786$, $p < 0.0001$). The narrow snouted *Platyoposaurus stuckenbergi* (Archegosauridae) occupied the most positive position, its palatine was a relatively simple shape, it was long and thin, slightly wider in the middle than at the ends. *Callistomordax kugleri* (Trematosauroidae), which had a broad skull with little snout in front of the nares, was at the opposite end of PC1 range (Figure 4.29), its palatine was orientated at a 45° angle to the anterior posterior axis, and it had a distinctive anterior split in the shorter shape. The taxa were not clustered on PC2, but with more towards the negative end of the axis (Figure 4.29). *Konzhukovia vestusa* (Archegosauridae) had the most positive position along PC2 (illustrated on Figure 4.29), though superficially it did not appear to be “wide”, the anterior portion of the palatine was wider than the posterior (Figure 4.29). At the negative end of PC2 was the palatine of *Eryosuchus garjainovi* (Capitosauroidae) which had a longer and more curved shape (illustrated on Figure 4.29).

Archegosauridae and Stem Stereospondyls dominated the positive end of the range for PC1; by contrast, the Rhytidosteoidea, Trematosauroidae and Capitosauroidae covered much of the length of PC1 range (Figure 4.30). The Archegosauridae were typified by a long and narrow palatine, with a posterolateral projection of the quadrate ramus of the pterygoid. Capitosauroids had a more uniform head width than the triangular skulls of the Rhytidosteoidea, which is reflected in the overall positions of palatal features. The ANOSIM ($R = 0.1707$, $P = 0.0006$) and PERMANOVA ($F = 4.831$, $P = 0.0002$) both showed significant differences in the palatine shapes of stereospondyls from different taxonomic groups. Pairwise comparisons of both tests showed significant differences between Archegosauridae and Trematosauroidae, Rhytidosteoidea (Table 4.12). Stem stereospondyls differed from Trematosauroidae. The ANOSIM identified a significant

difference between Capitosauroidae and Archegosauridae which were not significantly different according to PERMANOVA.

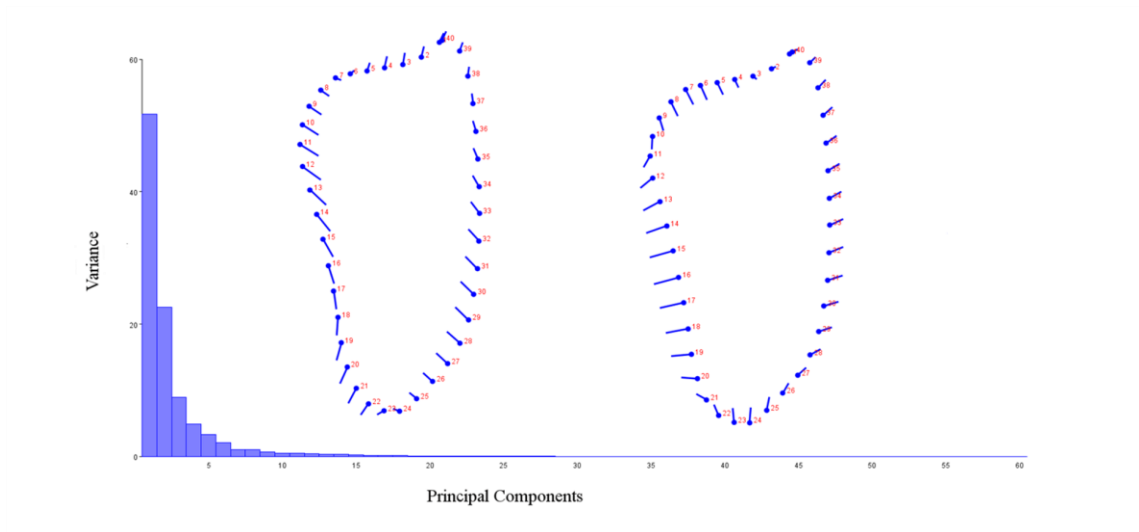


Figure 4.28 Variance explained by the Principal components of 40 semilandmarks around the palatine of 60 stereospondyl species. Scree plots of PC1 (left) and PC2 (right) are shown, the anterior of the palatine is toward the top of the page

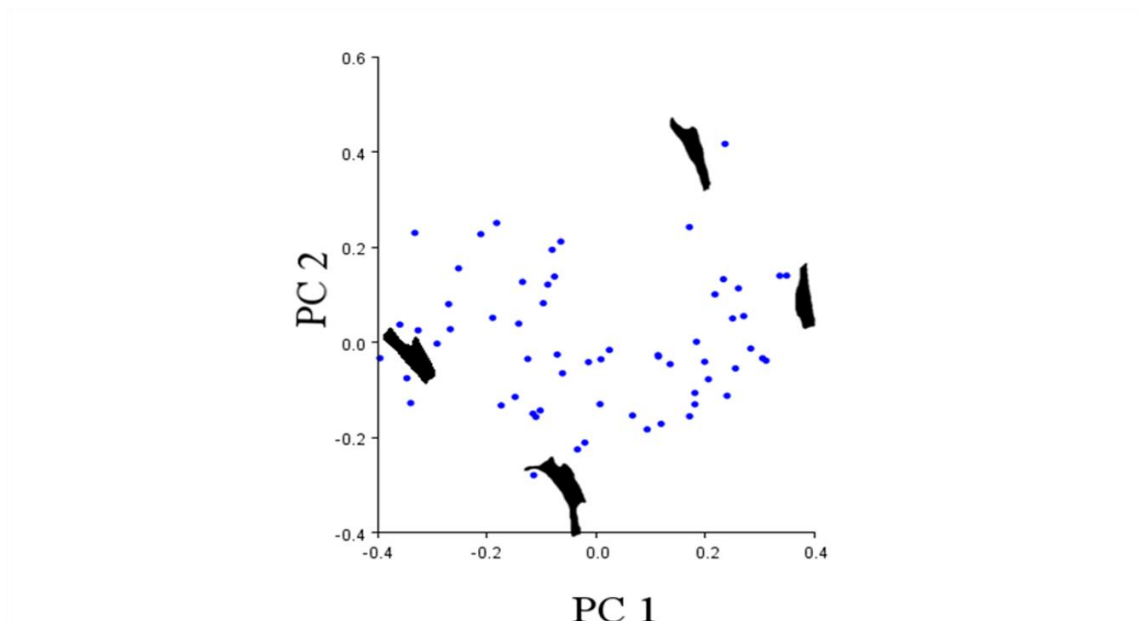


Figure 4.29 Position in morphospace of palatine shapes of 60 stereospondyls, along PC1 and PC2 based on 40 evenly spaced landmarks. *Platyoposaurus stuckenbergi* and *Callistomordax kugleri* palatine silhouettes illustrate the positive and negative extremes of PC1. *Konzhukovia vestusa* and *Eryosuchus garjainovi* illustrate the positive and negative extremes of PC2. A fully labelled plot is in electronic appendix EA 3

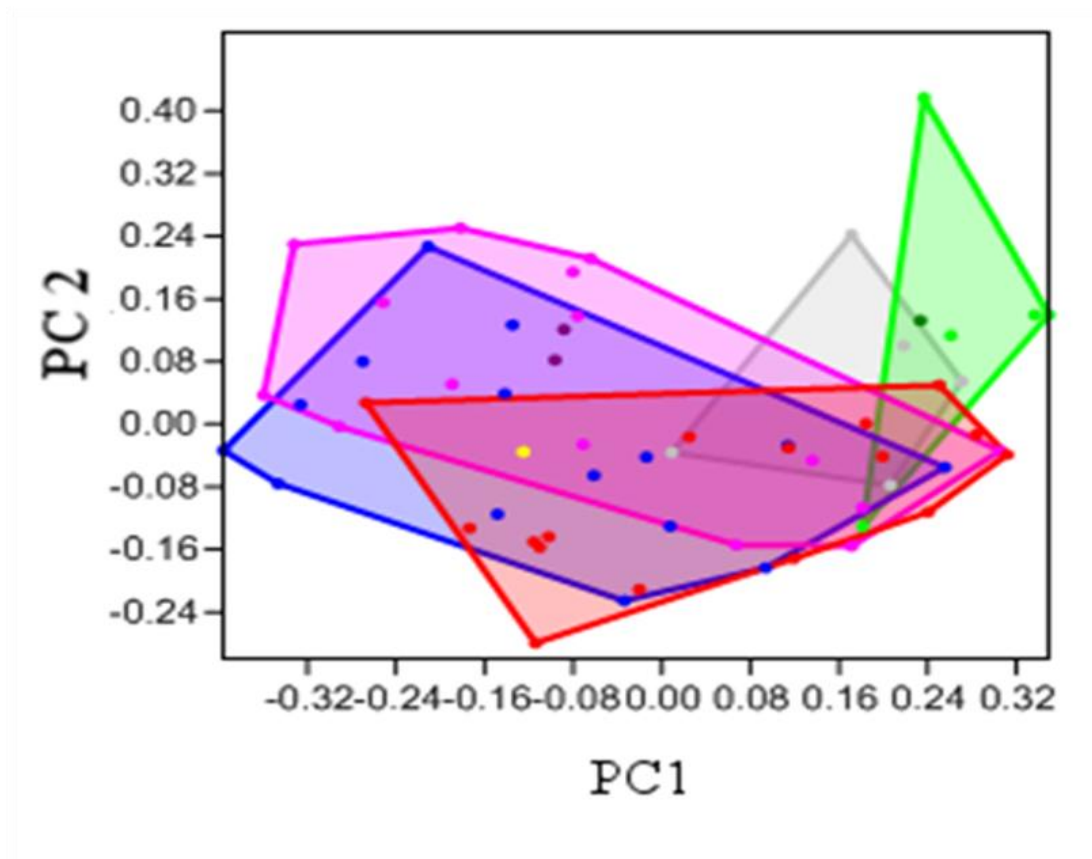


Figure 4.30 Position in morphospace of palatine shapes of stereospondyl species, along PC1 and PC2, based on 40 evenly spaced semilandmarks. Convex hulls delimit taxa according to their taxonomic group affiliation (as per Schoch and Milner, 2000); Archegosauridae - bright green, Trematosauroidae - blue, Rhinesuchidae-yellow, Stem stereospondyl - grey, Brachyopoidea - purple, Rhytidosteoidea - pink, Capitosauroidae - red, Plagiosauridae - dark green (single point).

Table 4.12 Pairwise comparisons of PC1 and PC2 scores of palatine outline semilandmarks, designated by taxonomic group. NPMANOVA values are above the diagonal and ANOSIM values are below the diagonal. Bonferonni sequentially corrected significant values are indicated in bold.

Abbreviations are as follows Stem = Stem stereospondyls, Arch = Archegosauridae, Brachy = Brachyopoidea, Plag = Plagiosauridae, Tremat = Trematosauroidae, Rhine = Rhinesuchidae, Rhyt = Rhytidosteoidea, Capit = Capitosauroidae

	Stem	Arch	Brachy	Tremat	Rhyt	Capit
Stem		0.3342	0.0481	0.0032	0.0343	0.0521
Arch	0.5512		0.0505	0.0004	0.0021	0.0018
Brachy	0.0426	0.0475		0.5068	0.9182	0.1094
Tremat	0.0098	0.0002	0.7779		0.325	0.0215
Rhyt	0.0694	0.0004	1	0.3493		0.0141
Capit	0.2247	0.007	0.0734	0.0424	0.0114	

4.3.10 Subtemporal vacuity shape using semilandmarks

The first two principal components accounted for 70% of the variation in the subtemporal vacuity (STV). PC1 represented 55% of the variance, PC2 was much lower at 15% (Figure 4.31). Levene's test showed that there was a significant difference between the variance distribution between PC1 and PC2 ($F = 17.326$, $P < 0.0001$). The 70 taxa showed a wide range in morphospace occupation along PC1 and PC2 (Figure 4.32). Variation in PC1 was associated with an overall lengthening and narrowing of the subtemporal vacuity (Figure 4.32). This is seen in *Vigilius wellesi* which was toward the highest positive values (Figure 4.32), which, despite its wide head, had a narrow subtemporal vacuity. *Kuttycephalus triangularis*, at the most negative position on PC1 had a subtemporal vacuity that is similar in shape to an equilateral triangle (Figure 4.32) PC2 showed an anteromedial expansion with an overall narrowing of the posterior portion of the subtemporal vacuity (Figure 4.32)

Deltasaurus kimberlyensis (Rhytidosteoidea) occupied the most positive position on PC2 (Figure 4.32), with a subtemporal vacuity that had a distinct widening on the medial margin. PC2 showed medial movement in the anterior portion, and a lateral movement of the posterolateral margin (Figure 4.32).

The Capitosauroidae, Rhytidosteoidea and Trematosauroidae all had large convex hulls, which were mostly positioned on the negative end of PC1 so they had much wider STV than the Brachyopoidea and Archegosauridae, which were responsible for the significant differences amongst the taxonomic groups (Table 4.13). Both statistical tests showed an overall significant difference, (ANOSIM $R = 0.08462$, $P = 0.0248$ PERMANOVA $F = 3.505$, $P = 0.0007$), but pairwise comparisons had no significant differences in the ANOSIM once sequential Bonferroni correction was applied. PERMANOVA showed differences between the Capitosauroidae and the Brachyopoidea and Archegosauridae, the latter two had narrow and elongate STV (Figure 4.33). Archegosauridae were significantly different from Rhytidosteoidea, the former had a range in morphospace that was much smaller and the Rhytidosteoidea exhibited STV that were wider and a range of shapes on the palate.

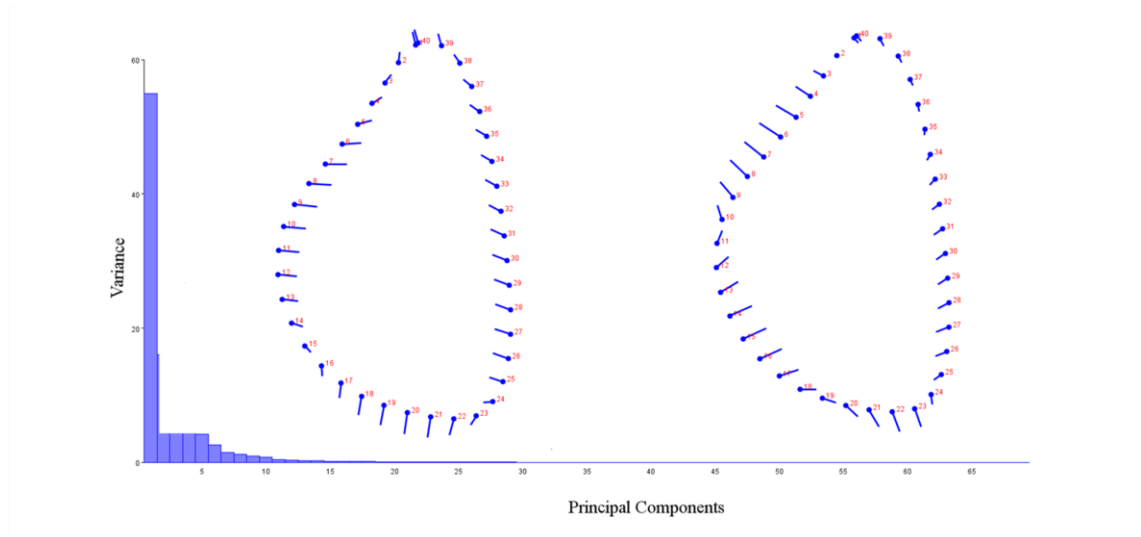


Figure 4.31 Variance explained by the Principal components of 40 semilandmarks around the subtemporal vacuity of 70 stereospondyl species. Scree plots of PC1 (left) and PC2 (right) are shown, the anterior of the subtemporal vacuity is toward the top of the page.

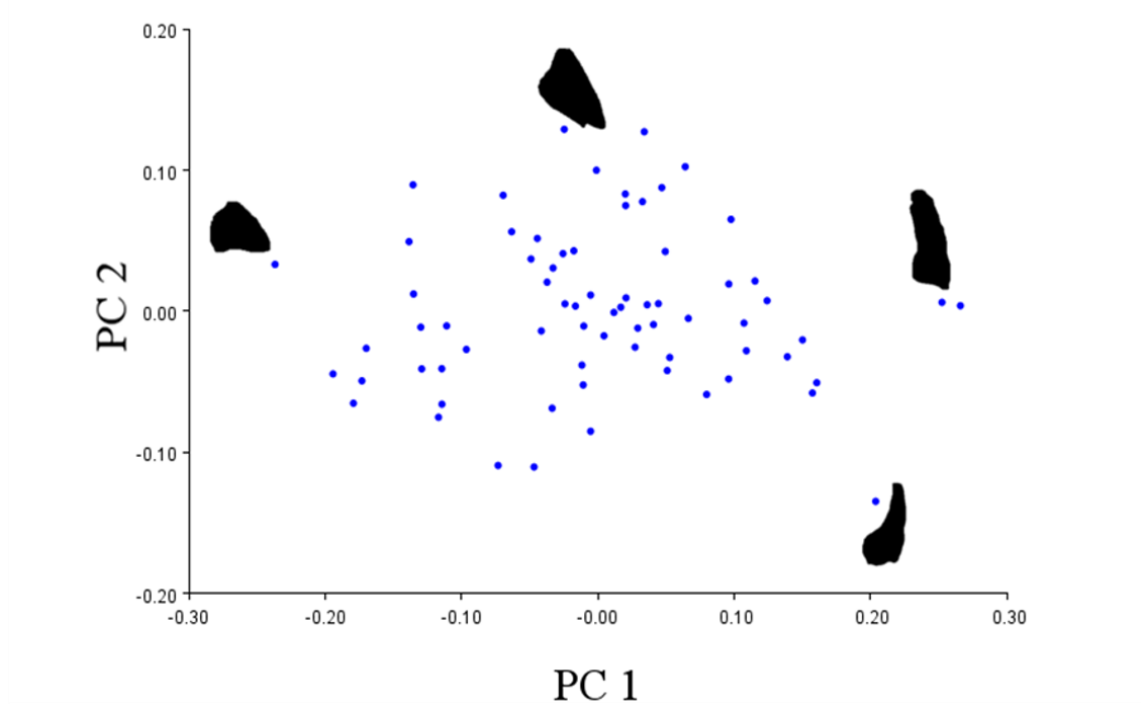


Figure 4.32 Position in morphospace of subtemporal vacuities of 70 stereospondyl species, along PC1 and PC2 based on 40 evenly spaced semilandmarks. *Vigilius wellsi* and *Kuttycephalus triangularis* subtemporal vacuity silhouettes illustrate the positive and negative extremes of PC1. *Deltasaurus kimberlyensis* and *Dendrorepeton arcadium* silhouettes illustrate the positive and negative extremes of PC2. A fully labelled plot is in electronic appendix EA3.

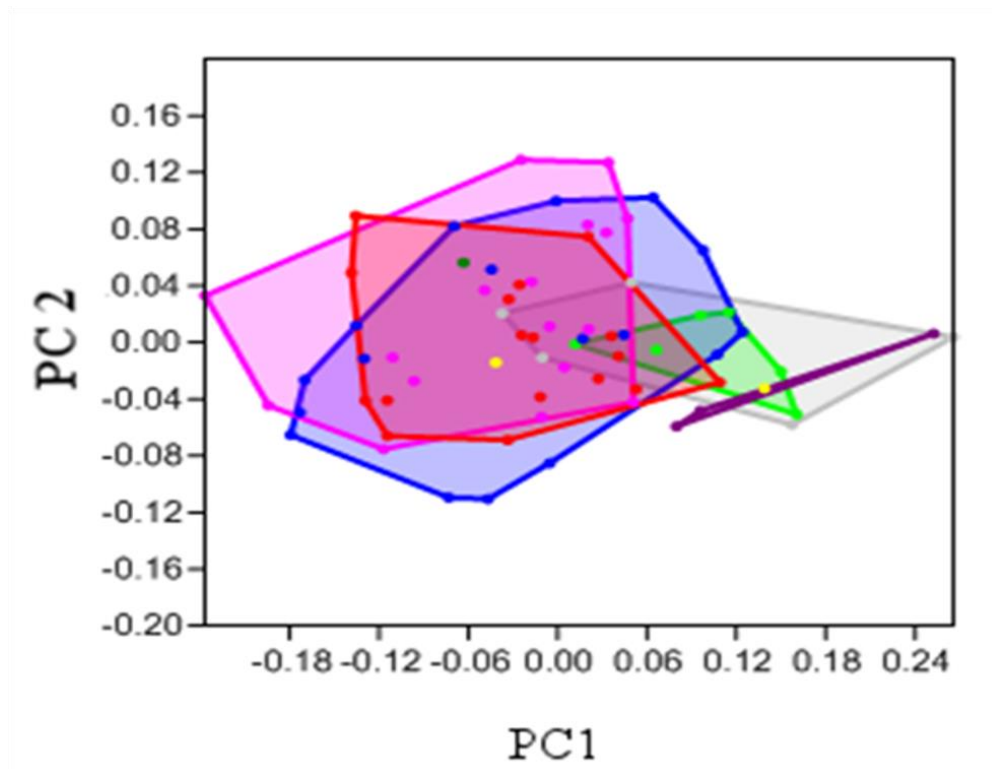


Figure 4.33 Position in morphospace of subtemporal vacuities of 70 stereospondyl species, along PC1 and PC2, based on 40 evenly spaced semilandmarks. Convex hulls delimit taxa according to their taxonomic group affiliation (as per Schoch and Milner, 2000); Archegosauridae - bright green, Trematosauroidae - blue, Rhinesuchidae-yellow, Stem stereospondyl - grey, Brachyopoidea - purple, Rhytidosteoidea - pink, Capitosauroidae - red, Plagiosauridae - dark green (single point).

Table 4.13 Pairwise comparisons of PC1 and PC2 scores of subtemporal vacuity outline semilandmarks, designated by taxonomic group. NPMANOVA values are above the diagonal and ANOSIM values are below the diagonal. Sequential bonferonni corrected significant values are indicated in bold.

Abbreviations are as follows Stem = Stem stereospondyls, Arch = Archegosauridae, Brachy = Brachyopoidea, Plag = Plagiosauridae, Tremat = Trematosauroidae, Rhine = Rhinesuchidae, Rhyt = Rhytidosteoidea, Capit = Capitosauroidae

	Stem	Arch	Brachy	Tremat	Rhine	Rhyt	Capit
Stem		0.8834	0.514	0.0508	0.7092	0.0195	0.0208
Arch	0.1689		0.4115	0.0086	0.4245	0.0019	0.0012
Brachy	0.7145	0.2091		0.0157	0.6011	0.0042	0.0022
Tremat	0.2922	0.1194	0.0404		0.4456	0.6671	0.9786
Rhine	0.9535	0.2043	0.803	0.6793		0.2454	0.2516
Rhyt	0.1767	0.0367	0.0213	0.6177	0.3013		0.5321
Capit	0.1414	0.0281	0.0217	0.371	0.3275	0.4224	

4.3.11 Mantel tests

Not all possible pairwise combinations were used as there is a certain amount of redundancy where some elements of one character also feature in the other, for example the skull outline and the tabular; palate and palatine. In other cases a correlation would not be informative of functional anatomy (Table 4.14), there would be little biological reasoning behind correlating the shape of the STV and that of the naris as they offer not real interaction in functional morphology. The PC scores of the discrete landmarks of the skull roof and palate were significantly correlated, demonstrating that the distance between stereospondyls in morphospace was the same for the skull roof as it is for the palate. From this we have an understanding that the skull roof and palate have changed at a similar rate across their taxonomy. If there was poor concordance between the two parts, then it would be suggestive of some elements of the anatomy being more disparate than others. The nares and the orbits changed in the same way as the skull outline, and as such also correlate with each other. The largest sources of variation in these three characteristics was a lengthening and narrowing and changing orientation of the orbits and nares, and in all cases there were significant differences between taxonomic groups. These correlations show us that the difference in the extent of narrowing of the skull between species is the same as the difference in the narrowing of the nares and orbit. This is not to say that the correlation between the matrices was perfect, but it was higher than it would be if it was random. Interestingly there was no correlation between the skull outline and the shape of the subtemporal vacuity, suggesting that the shape of the vacuity was driven by something other than overall skull shape.

4.3.12 Extant amphibians

PC1, which accounted for over 75% of the variance in the skull outline in dorsal aspect showed an overall lengthening and narrowing of the skull (Figure 4.34). PC2 showed a shortening of the snout combined with a posterior extension of the medial part of the posterior skull table, creating an overall more “flattened” posterior skull table as seen in *Ambystoma gracile*. As PC1 was accountable for so much variance, it has a much greater spread of values along its axis than PC2.

The most easily identifiable difference is between caecilians and anurans along PC1. The latter had relatively wider and shorter skull outlines. Urodeles drove the spread of values along PC2, thanks to the presence of the slightly unusual *Siren lacertina*.

When stereospondyls and a range of extant amphibians skull outlines in dorsal aspect were analysed by PCA the first principal component was accountable for ~65% of the variation in the 148 species (Figure 4.37). As with the independent stereospondyl and extant analyses, the combined outline analyses showed an overall lengthening and narrowing of the skull, where stereospondyls showed a much greater spread than extant amphibians. The narrow snouted stereospondyl *Aphaneramma rostratum* exemplified the most positive position on PC1 and the wide headed Brachyopoidea *Gerrothorax pulcherrimus* is at the negative extreme of PC1. PC2 showed a shortening of the snout and a flattening of the central part of the posterior skull margin at the positive end, where the shape can be seen in the caecilian *Typhlonectes compressicauda*. There was a significant difference in skull outline shapes between the two groups (PERMANOVA ($F = 16.4$, $P = 0.0001$) ANOSIM ($R = 0.1741$, $P = 0.0003$). Overall stereospondyls had a greater range in skull outline shapes, though extant amphibians occupied a similar range on PC2.

Table 4.14 Mantel test correlation output for selected aspects of stereospondyl anatomy

		Correlation R	P
Skull roof	Palate	0.2209	0.0201
Skull outline	Orbit	0.2209	0.0201
Skull outline	Naris	0.368	0.0001
Skull outline	STV	0.05179	0.2033
Orbit	Naris	0.1427	0.0075
Orbit	Lacrima	0.1724	0.0095
Ectopterygoid	Palatine	0.1058	0.028
Naris	Lacrima	0.1569	0.0227
Tabular	STV	0.02157	0.3257

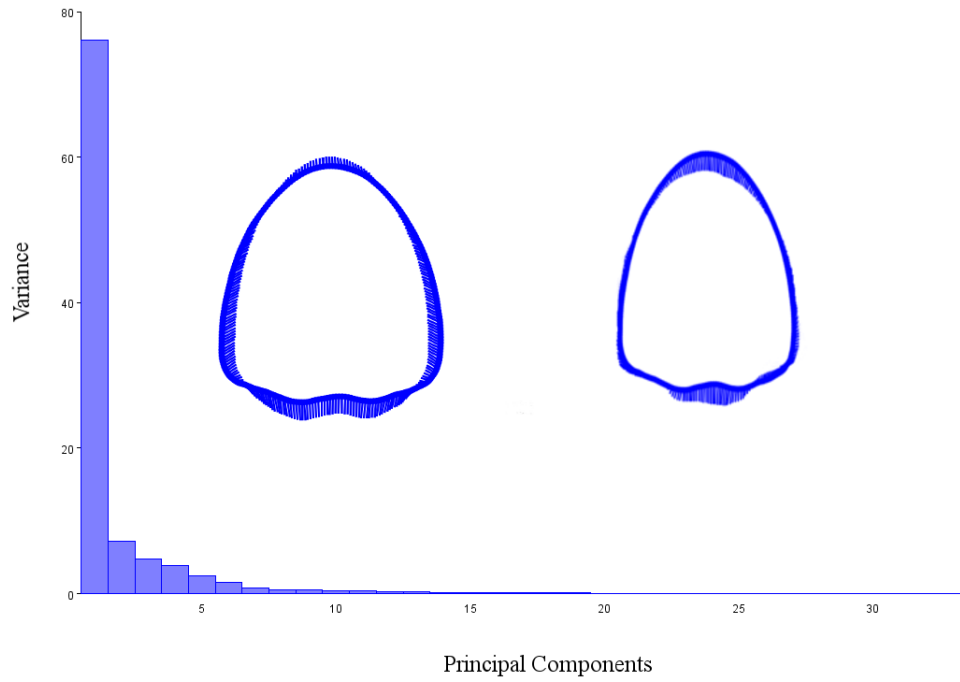


Figure 4.34 Variance explained by the Principal components of semilandmarks around the dorsal aspect of the skull roof of 34 extant amphibian species. Scree plots of PC1 (left) and PC2 (right) are shown, the anterior of the skull roof is toward the top of the page.

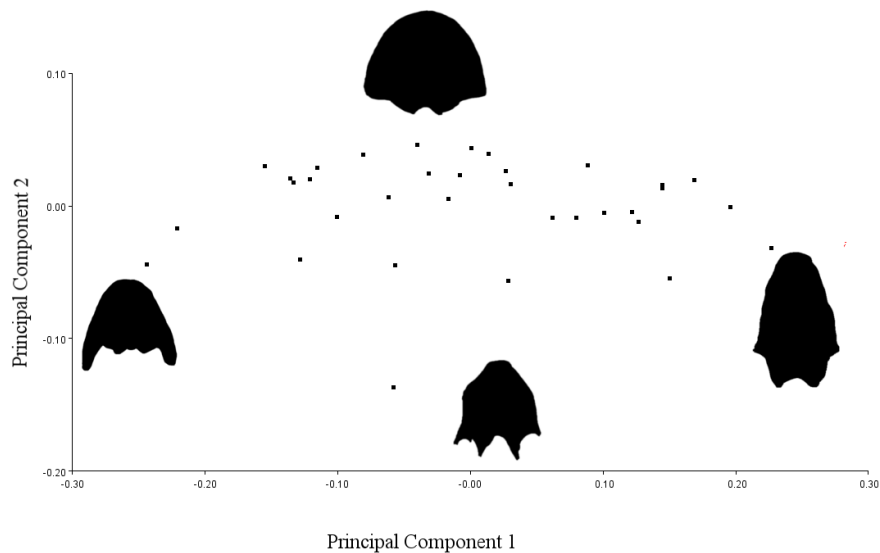


Figure 4.35 Position in morphospace of dorsal aspect of the skull roof of 34 extant amphibian species, along PC1 and PC2 based on 40 evenly spaced semilandmarks. *Indotyphlus battersby* and *Rana catesbeina* subtemporal vacuity silhouettes illustrate the positive and negative extremes of PC1. *Ambystoma gracile*

and *Siren lacertina* silhouettes illustrate the positive and negative extremes of PC2. A fully labelled plot is in electronic appendix EA 3.

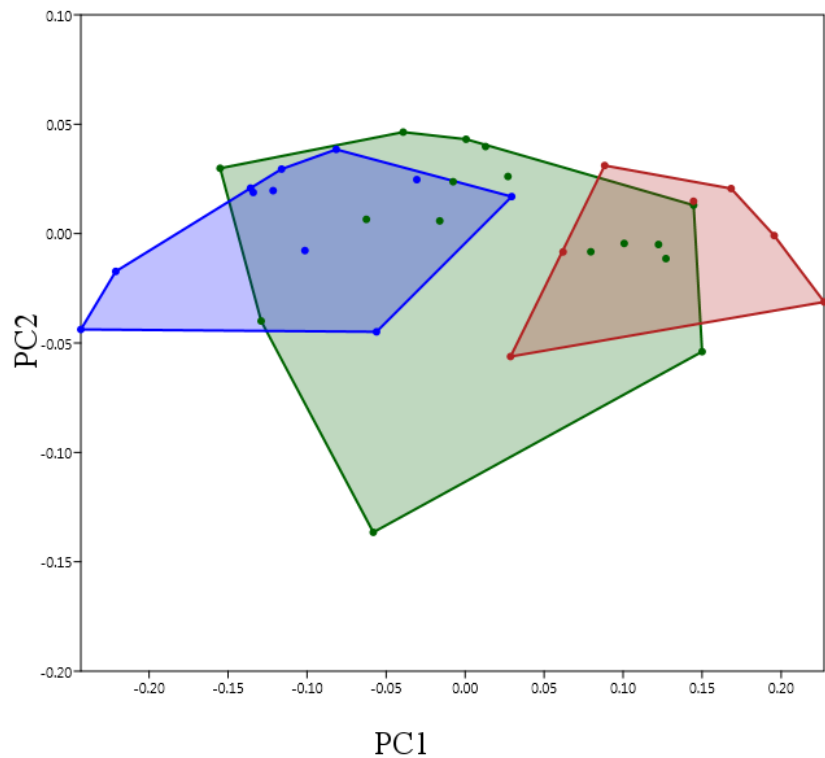


Figure 4.36 Position in morphospace dorsal aspect of the skull roof of 34 extant amphibian species, along PC1 and PC2, based on 250 evenly spaced semilandmarks. Convex hulls delimit taxa according to their affiliation; red: caecilians, blue: anurans, green: urodeles.

Table 4.15 Pairwise comparisons of PC1 and PC2 scores of extant amphibian outline semilandmarks, designated by group. NPMANOVA values are above the diagonal and ANOSIM values are below the diagonal. Sequential bonferonni corrected significant values are indicated in bold.

	Urodela	Caecilian	Anuran
Urodela		0.0122	0.0012
Caecilian	0.1493		0.0002
Anuran	0.0065	0.0001	

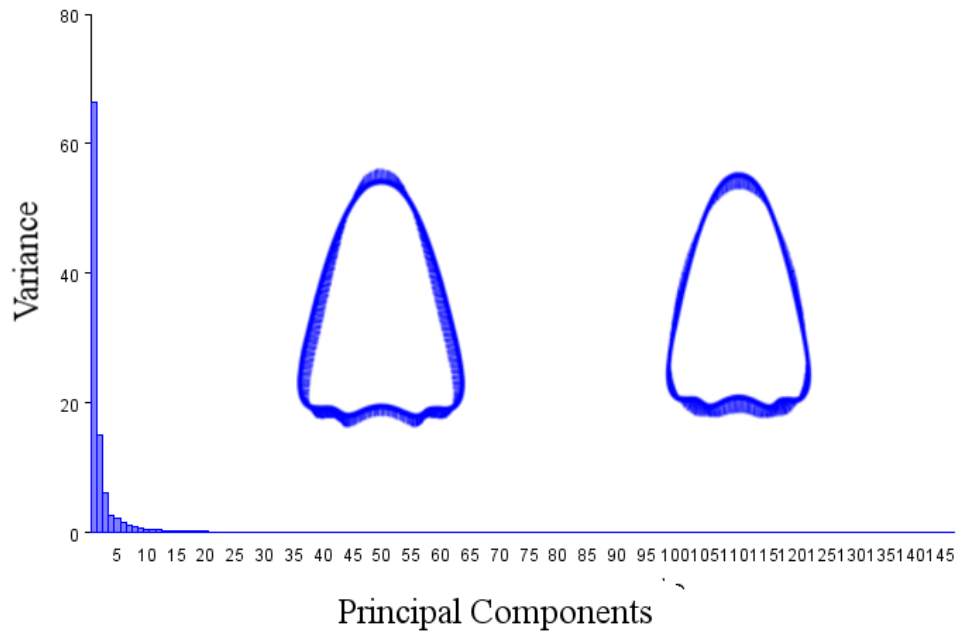


Figure 4.37 Variance explained by the Principal components of semilandmarks around the dorsal aspect of the skull roof of 34 extant amphibian species and 114 stereospondyl amphibian species. Scree plots of PC1 (left) and PC2 (right) are shown, the anterior of the skull roof is toward the top of the page.

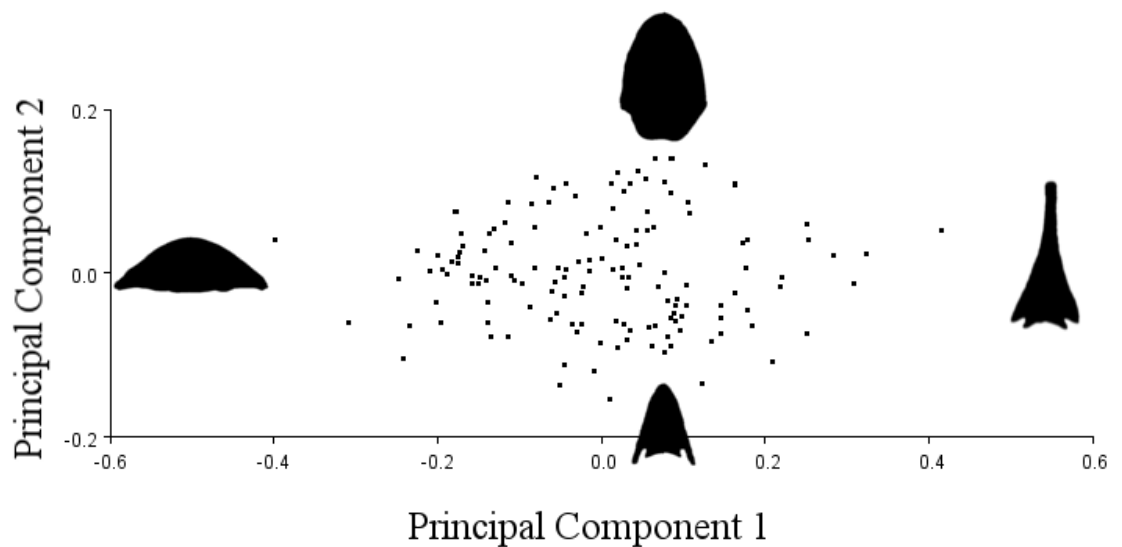


Figure 4.38 Position in morphospace of dorsal aspect of the skull roof of 34 extant amphibian species and 114 stereospondyl species, along PC1 and PC2 based on 40 evenly spaced semilandmarks. *Aphaneramma rostratum* and *Gerrothorax pulcherrimus* subtemporal vacuity silhouettes illustrate the positive and negative extremes of PC1. *Typhlonectes compressicauda* and *Microposaurus casei* silhouettes illustrate the positive and negative extremes of PC2. A fully labelled plot is in electronic appendix EA 3.

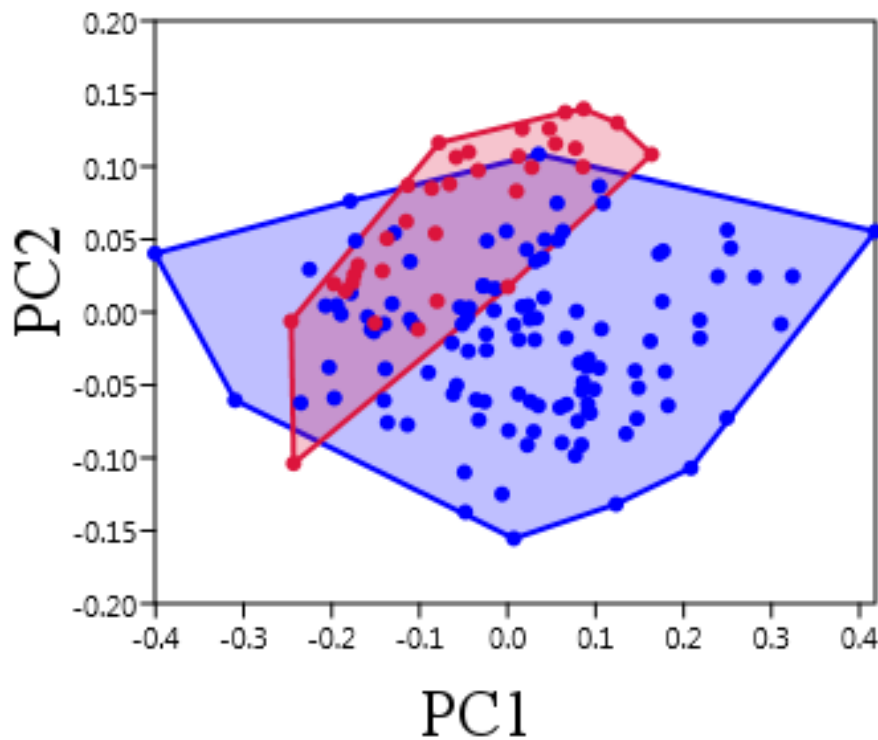


Figure 4.39 Position in morphospace dorsal aspect of the skull roof of 34 extant amphibian species (red) and 114 stereospondyl amphibian species (blue), along PC1 and PC2, based on 250 evenly spaced semilandmarks.

To gain further insight into the similarities and difference between extant amphibian groups, and stereospondyl taxonomic groups, the data were further divided into their smaller taxonomic components. There were significant differences in skull shapes between the groups (PERMANOVA $F = 19.42$ $P = 0.0001$, ANOSIM $R = 0.4166$, $P = 0.0001$; Figure 4.40 and Table 4.16), with concordance between the two tests in the pairwise comparisons. The Plagiosauridae were positioned at the negative end of PC1 due to their wide and short heads, they also occupied this position in the stereospondyl only analysis. The low numbers of individuals meant that though Plagiosauridae were significantly different from all other groups in the pairwise analyses, these differences were not robust enough to reach the threshold set by sequential correction. The inter stereospondyl group differences were very similar to the stereospondyl-only analysis, the differences in significance were driven largely by changes from the sequential corrections. Most interesting are the similarities and differences between stereospondyl groups and the extant amphibian groups. The Urodeles were significantly different from all other groups, excepting the previously discussed Plagiosauridae and caecilians, with which they substantially overlap on PC2, sharing similar shapes in the posterior skull

table, but caecilians had narrower skulls, as shown in the earlier analyses. The caecilians shared morphospace with the Trematosauroidae, particularly along PC1 where they overlapped with several of the wider snouted metoposaurs species such as *Koskinodon* and *Metoposaurus*. Anurans had wide and short heads, and so were not significantly different from the Brachyopoidea the latter also occurred closely in morphospace with the Japanese Giant Salamander. The Rhytidosteoidea shared a similar morphospace to the anurans on PC2, showing that they shared a similar range in shapes on the posterior skull margin.

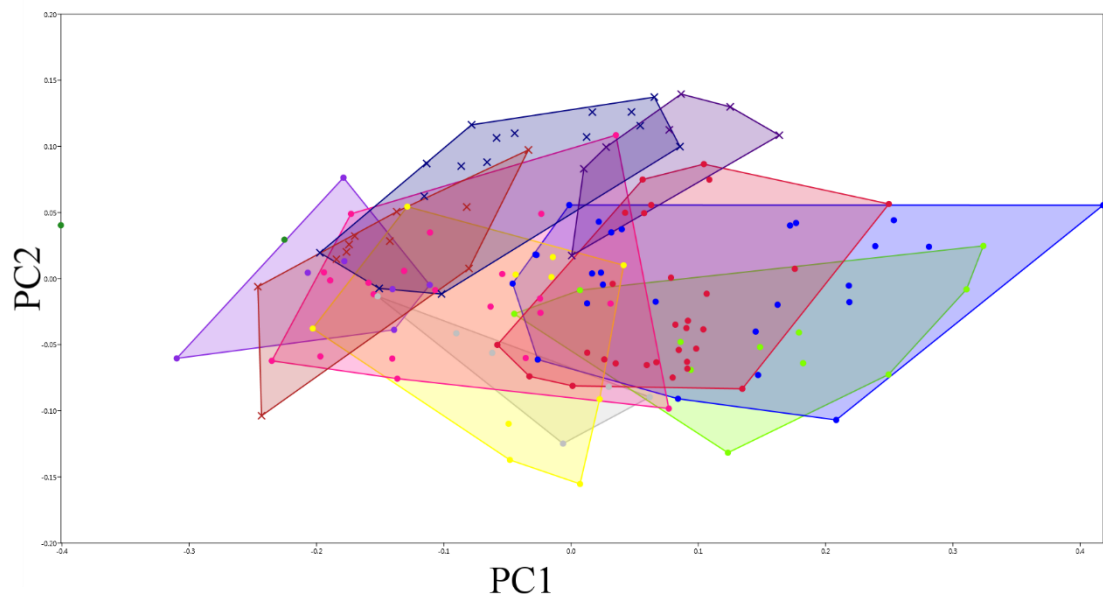


Figure 4.40 Position in morphospace of skull outlines of 114 stereospondyl species and 34 extant amphibians species, along PC1 and PC2, based on 40 evenly spaced semilandmarks. Convex hulls delimit taxa according to their taxonomic group affiliation; Stereospondyls marked with dots - Archegosauridae - bright green, Trematosauroidae - blue, Rhinesuchidae - yellow, Stem stereospondyl - grey, Brachyopoidea - purple, Rhytidosteoidea - pink, Capitosauroidae - red, Plagiosauridae - dark green. Extant amphibians marked with crosses: anuran - dark red, urodele - dark blue, caecilian - dark purple.

Table 4.16 Pairwise comparisons of PC1 and PC2 scores of extant and extinct amphibian skull outline semilandmarks, designated by taxonomic group. NPMANOVA values are above the diagonal and ANOSIM values are below the diagonal. Sequential bonferonni corrected significant values are indicated in bold.

	Stem	Arch	Plag	Brachy	Tremat	Rhine	Rhyt	Capit	Urodela	Anuran	Caecilian
Stem		0.0032	0.0343	0.0033	0.0029	0.7943	0.0565	0.0004	0.0002	0.0006	0.0017
Arch	0.0113		0.0133	0.0001	0.1686	0.0007	0.0001	0.0063	0.0001	0.0001	0.0009
Plag	0.0355	0.0156			0.0031	0.0172	0.0076	0.0024	0.0067	0.0391	0.0309
Brachy	0.0066	0.0002	0.077		0.0001	0.0016	0.0307	0.0001	0.0008	0.3912	0.0005
Tremat	0.0356	0.1988	0.0023	0.0001		0.0008	0.0001	0.1367	0.0002	0.0001	0.0236
Rhine	0.8675	0.0004	0.0148	0.0048	0.0206		0.0863	0.0001	0.0001	0.0015	0.0001
Rhyt	0.1969	0.0001	0.0248	0.5133	0.0001	0.0624		0.0001	0.0002	0.0493	0.0002
Capit	0.007	0.004	0.0027	0.0001	0.0028	0.0003	0.0001		0.0001	0.0001	0.0001
Urodela	0.0001	0.0001	0.0061	0.0014	0.0001	0.0002	0.0004	0.0001		0.001	0.0072
Anuran	0.0015	0.0001	0.0888	0.491	0.0001	0.0006	0.3045	0.0001	0.0061		0.0001
Caecilian	0.0013	0.0003	0.0263	0.0003	0.1132	0.0002	0.0002	0.0001	0.046	0.0001	

4.4 Discussion

4.4.1 General observations

All elements of skull anatomy that were assessed here showed at least some significant differences between the taxonomic groups, which is not surprising since taxonomic procedures use some of these features to assign species (see list of apomorphies in chapter 2). Pairwise comparisons showed that several taxonomic groups were more closely affiliated each other than with others. This present investigation has shown that geometric morphometrics can be a useful tool to objectively quantify shape changes in stereospondyl skull anatomy.

Since Principal Component Analysis is designed to highlight the areas of greatest variance, it can be seen that the relative length and width of the skull (as the effect of size was removed) and its components changed frequently amongst both stereospondyls and extant amphibians. Another common occurrence was the forward movement of one side of the feature, coinciding with a backward movement of the other side, essentially moving from a straight orientation to a diagonal one. This type of movement was a change in orientation of the bone or orifice, from a straight anterior/posterior orientation to a diagonal one whilst also becoming elongated. This was picked up in the analyses because the starting point of the outline analyses was always the centre of the anterior most point of the element. In almost all of the analyses here, the biggest changes in shape are a narrowing or a change in orientation. This means that the biggest difference between stereospondyls was the width of the skull, which was not restricted to the rostrum, and the orientation of specific features, including the orbits, nares, tabular and lacrimal, which are not necessarily directly linked to a change in the width of the skull.

The positions of the orbits, nares and choanae were a source of considerable variation in the analyses of discrete landmarks, as indicated by the long “sticks” on the scree plots which are a visual representation of the Eigen values. There is also an overall narrowing of the skull. These changes could demonstrate different capabilities in prey seeking behaviour, reflected through vision and biting (Fortuny et al., 2011, Maganuco, et al., 2014, Fortuny et al., 2016). The taxonomic groups were frequently retrieved in the discrete landmarks, despite overlap in the centre of the principal component plots, both for the skull roof and the palate, so the relative positions of the nares and orbits on the skull roof are important to the assignment of taxonomic groups.

The palate is very important to the assignment of taxonomic groups (see chapter 2). The position of the posterior most point of the exoccipital and the shape of the subtemporal vacuities seems to be important for the taxonomic group separation of the palate features. The subtemporal vacuity does not feature heavily in character based phylogenies (Schoch, 2000; Warren and Marsicano, 2000; Warren et al., 2011), and the posterior extent of the exoccipital only fares a little better, (Landmark 26, figure 4.2, Bolt and Chatterjee, 2000; Schoch, 2000; Warren and Marsicano, 2000; Damiani, 2001; Damiani and Yates, 2003; Warren et al., 2011), in spite of their importance in bite abilities and neck orientation. The exoccipital has only been incorporated into the taxonomy of the Brachyopoidea (Warren and Marsicano, 2000), which were not featured in the discrete palatal analysis because they had insufficient numbers of species with well-preserved palates.

The separation of taxonomic groups is less clear in the outline analysis than the discrete analyses, which is largely driven by the scaling over binary nature of PCA, which serves to highlight the similarities between the taxonomic groups used by Schoch and Milner (2000). Each taxon in a PCA has its own unique scores, whereas character based phylogenies assign the taxon to fewer categories, typically two to three. The scaling showed us that there was much more preorbital/rostral variation than simply “less than twice the length of the posterior skull table, and more than twice the length of the posterior skull table (Schoch and Witzmann, 2009) and species fall along the full length of this scale. This is not to say that all character based assessments are without use, many characters deal with clearly binary characteristics, like the presence or absence of a bone on the skull table, but in the case of shapes the scope of PC scores is greater.

The extent that different groups spread along the PC scales differed. The skull shape of the Capitosauroida varied minimally in relative length and width, but the posterior skull margin, represented in PC2 was diverse in this group. The posterior skull margin is not a part of Capitosauroida taxonomic association (Schoch and Milner, 2000), most probably because there is overlap by almost all taxonomic groups. The posterior skull margin showed more variance than proposed by Steyer (2002) (slightly concave / semi-circular), Damiani (2001) (posterolateral skull corners anterior / posterior to distal end of tabular horn) and Schoch (2008) (cheek posterior to tabular horns / at one level). Given the variance there is very likely a functional significance which will be discussed later.

Although there were significant differences amongst taxonomic groups for all of the ten anatomical features assessed here, the pairwise comparisons do not show consistent differences between all combinations of taxonomic groups. The most common difference

between taxonomic groups was between the Brachyopoidea and the Capitosauroida. The latter is frequently considered the most derived of the stereospondyls, but the former has the longest duration in the fossil record. Frequently the early Archegosauridae differed from the Rhytidosteoidea and Capitosauroida.

The Rhinesuchidae were frequently not different from any other group, and the Capitosauroida were only different from the equally numerous Trematosauroida on two occasions. The Capitosauroida frequently had a much smaller morphospace than the Trematosauroida. It is worth taking a moment to consider the unusual disparity of one of the most speciose groups, the Trematosauroida. The trematosauroids are considered by several authors to be at least paraphyletic if not polyphyletic (see Yates and Warren, 2000; Maganuco et al., 2014). The metoposaurs are trematosauroids from the Middle and Late Triassic, and unlike species from the Early Triassic, they have relatively wider heads with more anteriorly placed orbits. They are the source of much of the morphospace range amongst the Trematosauroida supporting the character based phylogenies that illustrate paraphyly.

The orbits were typical of many other physical features, the two biggest shape changes were an overall narrowing, and a change in orientation from straight (parallel to the long axis of the skull) to diagonal. There is little to differentiate the orbit shape of stereospondyl taxonomic groups, they substantially overlap. This concurs with the general phylogeny approach as the only reference to the orbit shape comes from Steyer (2002), who refers to them as 0) rounded or 1) not. The position and size of the orbit are featured much more frequently (see Yates, 1999; Yates & Warren, 2000; Bolt and Chatterjee, 2000; Schoch, 2000; Warren and Marsicano, 2000; Damiani, 2001; Steyer, 2002; Steyer, 2003; Damiani and Yates, 2003; Schoch et al., 2007; Schoch, 2008; Warren et al., 2011). The position of the orbit was a source of considerable variation, shown in the discrete analysis, stereospondyls exhibit more orbit morphological variation than the discrete positions of orbits that are used in character phylogenies (Bolt and Chatterjee, 2000; Schoch, 2000; Yates and Warren, 2000; Steyer, 2003). This was more than a change in the shape of the rostrum, many Trematosauroida metoposaurs had an elongated preorbital skull table. Several Rhytidosteoidea and Trematosauroida species had orbits that were much closer to the lateral skull margin than the midline. These scaled position changes could be indicative of functional differences between these species, and will be considered in more depth in chapter 6.

The small and central morphospace occupation of naris outline by the numerous Capitosauroidae is interesting. Considering the species number, geographic and temporal range of this group, it is surprising that their naris morphology is so conservative, particularly when for the Trematosauroidae it is so diverse. The Trematosauroidae have much more skull outline disparity and skull roof discrete disparity than the Capitosauroidae, resulting from the inclusion of the metoposaurs. The orbits and nares correlated with each other and the skull outline morphospaces. This is not to say that skull outline shape determines the naris or orbit, but it does show us that the selective pressures acting on skull shape could be causing the same rate of change on the orbit and naris. The naris has been a popular character in phylogeny studies (Schoch, 2000; Damiani, 2001; Yates and Warren, 2000; Morales and Shishkin, 2002; Schoch and Witzmann, 2009; Dias da Silva and Marsicano, 2011), but given the considerable overlap and overall correlation with skull shape, perhaps it should be considered with more caution in phylogeny reconstructions.

The lacrimal is used in the assignment of species to the stem stereospondyls, and the Rhytidosteoidea (Schoch and Milner, 2000), though the latter is because they supposedly do not have lacrimals, which is not the case. The lacrimal appears in most phylogeny studies but most authors are concerned only with its presence (Bolt and Chatterjee, 2000; Warren and Marsicano, 2000; Yates and Warren, 2000; Damiani and Yates, 2003; Damiani and Warren, 1996; Schoch, 2008; Dias da Silva and Marsicano, 2011) and only Schoch and Witzmann (2009) with its shape. Here, the lacrimal shows the same changes as the orbit and naris, narrowing on PC1 and diagonal orientation on PC2 and was correlated with both. The statistical significance amongst taxonomic groups was driven by the consistent lacrimal shape of the Capitosauroidae, who have limited disparity in length and width. The overlaps of convex hulls of the lacrimal indicated that shape variation that was much more substantial than the discrete character states that have been traditionally used to assign species to their phylogenetic positions. It would appear that lacrimal shape is a result of the skull shape changes but it also correlates with the morphospace of the orbit. As the orbits are the area of greatest weakness in the skull table (Fortuny et al., 2015) and the lacrimal changes shape in accordance with the orbit and skull shape, it may well play a role in the stabilisation and strength of the skull. Long and flat skulls are vulnerable to bending forces when they are lifted (Penrice and Ruta, 2017). An additional bone could spread the stress across the skull table (Fortuny et al., 2011; Marce-Nogue et al., 2015) and decrease deformation from bending.

The tabular bone, which formed part of the otic notch / squamosal embayment, is widely used in the phylogeny reconstructions (Damiani and Warren, 1996; Marsicano, 1999; Bolt and Chatterjee, 2000; Yates and Warren 2000; Schoch, 2000; Damiani, 2001; Steyer, 2003; Schoch, 2009; Schoch, 2008; Dias da Silva and Marsicano, 2011; Warren et al., 2011). Here, the biggest source of shape change is the change in orientation, going from a posteriorly orientated at the positive of PC1 to an almost lateral orientation. PC2 shows a widening in the positive direction. In spite of its wide use in phylogeny studies, the tabular shows little distinction between taxonomic groups, the significance is driven by the tabular of Brachyopoidea, whose tabulars do not form horns, but only created a small bump in the posterior margin of the skull. The phylogeny studies tend to focus on the formation of the horn, and not the entire shape of the bone, which is what has been done here. It is possible that the phylogeny studies have placed too much emphasis on the tabular, considering its lack of distinction between taxonomic groups. However phylogeny studies do not seek to only assign taxa to taxonomic groups, but to positions within taxonomic groups within a wider phylogeny. As there is substantial within group variation there is the possibility that the shape of the tabular may be evolutionarily driven by functional constraints of the environment rather than by phylogeny. To determine how these shapes change between individual a range of clustering analyses could be carried out, such as k-means clustering, neighbour joining or classical means clustering will identify significant groups of tabular (or any other characteristic) shapes which can then be examined for commonalities between the species such as size or environment.

PC changes for the ectopterygoid followed the same narrowing and orientation change that was seen in the orbit, naris and lacrimal. The dentition of the ectopterygoid is the focus of characters in phylogeny studies (Damiani and Warren, 1996; Yates, 1999; Bolt and Chatterjee, 2000; Yates and Warren, 2000; Damiani and Yates, 2003). Although there was overlap of the taxonomic group morphospaces, there were some clear distinctions, such as the short and wide Brachyopoidea at the negative end of PC1, and the Permian stem and Archegosauridae were consistently in the positive area of PC1.

The palatine and ectopterygoid correlated in morphospace, demonstrating the two bones differ to the same extent between species. The position of the palatine on the palate means that it is bordered by several bones as well as the interpterygoid vacuities and the choanae. These influences have resulted in the palatine occupying a large range of morphospace with a well spread distribution across both PCs. The major changes were again a change in orientation (PC1) and a widening (PC2). The taxonomic group distinction lay with the

Archegosauridae, who possess a very simple rod shaped palatine, with no anterior expansion anterior to the interpterygoid vacuity, and its suture with the ectopterygoid is straight transverse. The stem Stereospondyls also had seemingly simple palatines. The majority of palatine characters in the literature have been focussed on the dentition (Yates, 1999; Bolt and Chatterjee, 2000; Yates & Warren 2000; Schoch 2008) and occasionally the sutures with other bones are used (Yates, 1999; Schoch and Witzmann, 2009). The sutures and dentition are clearly important characters for both distinction and functionality. The shape of this bone might not follow the group affiliations, but its shape is strongly indicative of its strength, and considering its placement on the palate, may be an ideal candidate for further detailed investigation, such as FEA. Fortuny et al. (2015) and Lautenschlager et al. (2016) amongst others demonstrated that suture and vacuity positions are key in the distribution of stress across the skull and palate. As the simplest palatine occurred in early stereospondyls, it is possible that the evolution of complex palatines could be a response to diversification of prey seeking through their evolution. The complexity in the palatine increases as more stereospondyl morphotypes appear in the fossil record.

The subtemporal vacuity showed weak differentiation by group, but pairwise differences still existed, particularly driven by the unwidened shapes of the very early Archegosauridae (Permian) and the much later Brachyopoidea (*Vigilius welllesi* is from the Late Triassic of North America). The Trematosauroidae, Capitosauroidae and Rhytidosteoidea had more medially widened subtemporal vacuities. There was no tendency for anterior or posterior widening of the subtemporal vacuity, as these taxonomic groups were distributed along the length of PC2. Few authors have attempted to characterise the subtemporal vacuity, which is no surprise considering the substantial variation it shows (see Schoch, 2000; Warren and Marsicano, 2000; Warren et al., 2011). Interestingly, this vacuity shape is not correlated with the skull outline shape, stereospondyl species with similar shaped skulls do not exhibit the same degree of similarity in subtemporal vacuity shapes. The STV is where jaw adduction muscles pass through the palate to the lower mandible. The composition of these muscles varies between extant and extinct species and is discussed more thoroughly in Chapter 6.

The structures that have been investigated are a combination of purely structural and those that have musculature associations. In most cases the methods used have been able to highlight differences between taxonomic groups or illustrate high levels of concordance

between them. The PCA has shown us that the structural and muscle supporting structures all have substantial shape variation across their range.

4.4.2 Extant amphibian skull shapes

Extant amphibian studies that use geometric morphometrics tend to be much more narrowly focussed than the one carried out here. Nevertheless there is sufficient within group variation to be able to identify disparity in anurans (Clemente-Carvalho et al., 2008; Escoriza and Hassine, 2014), urodeles (Ivanovic et al., 2007; Ivanovic et al., 2009) and caecilians (Sheratt et al., 2014; Hetherington et al., 2015). The purpose of the amphibian studies varied, so their approach to which areas of the skull were investigated differed but all used discrete landmarks. Unfortunately when using discrete landmarks all specimens must have the same comparable positions. Since stereospondyl anatomy is so different from extant amphibian anatomy (discussed in Chapter six), the discrete landmark approach could not be used. However the dorsal skull outline analysis was far from uninformative. There are two key messages to be taken from this brief study of extant amphibian skulls. Firstly, it is possible to distinguish between the major groups of amphibians based on their dorsal skull outline, and secondly, stereospondyls far exceed extant amphibians in variation of skull outlines.

Of course only a small sample of extant amphibians were used in these analyses, but they used a range of families and life history characteristics. The difference in the narrowed skulls of the subterranean caecilians was markedly different from the anurans. The anurans were represented by terrestrial, arboreal and aquatic species. Caecilian skulls are adapted for burrowing and so need to be strong and structured in a way to reduce resistance in burrowing, which they have achieved by having a solid skull table and an anteriorly narrowed skull (Sheratt et al., 2014). The narrowed caecilian skull was no match for the Trematosauroidae and Archegosauridae, both of which had much longer rostrums and narrower post orbital skull tables. The comparative anatomy of these groups is discussed in chapter 6.

There was an area of morphospace that was shared by urodeles, anurans, Brachyopoidea, and Rhytidosteoidea. The common shape was roughly that of an isosceles triangle, with a narrowing at the orbit to the rostrum. The majority of extant amphibians in this space were terrestrial and arboreal. Tree frogs such as *Nyctixalus pictus*, *Theloderma stallatum*, *Phyllatus signatus* and *Philatis microtypanum* were closely associated with

Rhytidosteoidea and Brachyopoidea species *Siderops kehli*, *Bracyops laticeps* *Kestrosaurus australis*. With the exception of *S. kehli*, the remainder of the stereospondyl species in this cluster were small by stereospondyl standards, though not as small as the extant amphibians.

4.4.3 Functional implications of shape differences

Ecomorphotypes were clearly delimited in Fortuny et al., (2011), though only visually, not statistically. These ecomorphotypes (terrestrial, amphibious, and aquatic) were assigned on the basis of skull shape, where narrow skulls were aquatic, and wider skulls were either amphibious or terrestrial. None of the stereospondyls used in the Fortuny study were assigned a terrestrial mode of life, but the Rhytidosteoidea and Rhinesuchidae were not included by Fortuny et al., (2011). The skull outline differences here showed a similar distribution in morphospace to the skulls in Fortuny et al., (2011). I did not preassign ecomorphotypes to the skulls because the number of species used in this analysis was substantially greater than the Fortuny et al., study and the level of information that would be required to determine the ecomorphotype is not available for all of these species. This present work could be used as a platform for future works that aim to use further skeletal data (e.g. long bone formation, rib morphology) in conjunction with a cluster analysis of skull shapes to assign ecomorphotypes.

Skull shape impacts key features of stereospondyl palaeobiology, in particular in association with movement and prey acquisition (Fortuny et al., 2011; Bates and Falkingham, 2012; Marcé-Nogué et al., 2015). Skull shape will affect resistance in water and less so in air, as well the bite strength (Fortuny et al., 2011; Penrice and Ruta, 2017). A triangular head shape would be efficient for swimming (Fortuny et al., 2011), but with this narrowing would be a reduced bite force (from skull strength). Of course this concerns the overall 3D shape of the skull and stereospondyls should not be considered in only a 2D perspective, but almost all of their skulls were greatly flattened (Yates and Warren, 2000; Fortuny et al., 2011; 2015).

The Archegosauridae and some (non metoposaur) Trematosauroidae had very similar morphospace occupations for skull shapes. It is possible that these groups may have employed a rapid lateral head movement to acquire prey, based on a narrow snout that would encounter less resistance in water (Fortuny et al., 2011; Schoch, 2014). I would

require further evidence to be certain of this and feeding actions are discussed more fully in chapter six of comparative anatomy.

The large head of Capitosauroida would be able to withstand a reasonable amount of strain without breaking (Fortuny et al., 2011, 2015), suggesting that the Capitosauroida may be able to deliver a formidable bite. The feeding action of the Capitosauroida has been reassigned several times, from benthic ambush predators (Ochev, 1966) who used suction feeding (Watson, 1958) to suction feeding in conjunction with active swimming as proposed by DeFauw (1989). The suction feeding hypothesis has been largely rejected on the basis that stereospondyl skulls were akinetic and flattened (Schoch and Milner, 2000) and lack the short parabolic skull of optimal suction feeders (Damiani, 2001). Large skulls impede the suction ability so cannot produce a force sufficient to catch swimming prey (Damiani, 2001). If this is the case then we must consider the Capitosauroida in conjunction with more suitable modern analogues to determine its most likely palaeobiology.

The Rhytidosteoidea skulls were not sharply narrowed in the preorbital area, but there was some preorbital narrowing. The skull was not well shaped for rapid swimming (Fortuny et al., 2011). The Rhytidosteoidea were generally smaller than the Trematosauroida and Capitosauroida (detailed further in chapter 5). Larger skulls have weight considerations to adapt to, so perhaps the smaller Rhytidosteoidea were adapted to terrestrial living, and this was initially proposed by Jeannot et al. (2006) and later supported by McHugh (2015). Several Rhytidosteoidea match the skull shapes of arboreal and terrestrial extant amphibians. The Rhytidosteoidea would not have needed the buoyancy of the water to support their weight, and would be able to acquire small terrestrial invertebrates as they could keep them within their field of vision with their anteriorly placed orbits as has been demonstrated in other species (Damiani, 2001; Heesy, 2004; Stevens, 2006). Alternatively, they may have sought slow moving hard-shelled prey, as suggested by Maganuco et al., (2014).

The Trematosauroida had the greatest range of morphospace occupation and ranged from having orbits and nares that were close to each other, to being much more distant. The most garial-like types belong to the Trematosauroida. The metoposaurs are reported by some to form their own clade in phylogenetic analyses (See Yates and Warren, 2000; Maganuco et al 2014) making a paraphyletic Trematosauroida. The paraphyly is reflected here in the substantial disparity found amongst the Trematosauroida. Their narrow preorbital skull tables were well adapted to piscivory, as they would have minimal

water resistance in a lateral swipe (Grigg and Kirshner, 2015), though the widened posterior skull table would decrease efficiency in a rapid forward movement. The preorbital skull table in these narrow snouted Trematosauroida is the weakest shape amongst stereospondyls (Fortuny et al., 2011), so it is poorly suited to hard or struggling prey. This leaves it with few other options than piscivory. This will be examined more closely in the comparative anatomy chapter. The metoposaurs, with anterior orbits probably had one of the largest fields of vision amongst the stereospondyls. The orbits are the weakest part of the skull (Marce-Nogue et al., 2015), and it would seem that there is considerable overlap in the toothrow and the orbit positions.

The tabular was positioned on the posterior margin of the skull table, so was less likely to be affected by the types of skull shape changes we have seen here. The main change was the change to the orientation, consistent with the otic notch closure (as in *Quasicyclotosaurus campi*, Capitosauroida, outlined in Figure 4.4.2). Despite this distinctive feature, the stereospondyls with closed or narrowing otic notches (all of which were in the Capitosauroida) did not cluster close to each other in morphospace. The function of the tabular horn has been suggested as a muscle attachment site for a head lifting muscle that attached to the clavicles. If this was a true structural functional adaptation, we would have expected clearer delimitations in morphospace that were associated with a particular head shape.

The orbit position will affect the field of vision and the visibility of the prey in acquisition (Damiani, 2001). Laterally placed orbits indicate that a species could see through the water column to either side of their head and not just above themselves, and behind, in the case of terrestrial vertebrates, orbits that were close to each other would have more binocular vision, but a smaller field of vision (Grigg and Kirshner, 2015). The Permian had stereospondyls with orbits that were in the posterior half of the skull, which was a similar shape to an isosceles triangle. These orbital position suggests that these species may have had some lateral vision, but the amount of preorbital skull may interfere with a forward biting action as the bones may have obstructed with the field of vision in flat stereospondyl skulls (Damiani, 2001, Schoch et al., 2014).

It is worth noting that the morphospace of the Capitosauroida was unusually small in the discrete landmark analyses, particularly as they are so numerous. Their orbits and nares were distant from each other, creating a large mid skull table area. The posterior orbital placement could restrict their vision to above them or directly lateral (as in crocodiles), certainly not below them (Damiani, 2001, Schoch et al., 2014). The Rhytidosteoidea had

little variation on PC2 and occupied the top half of PC1 in the discrete skull roof analysis. This puts them in the top range for orbits and nares being close, meaning that there is minimal interference by the preorbital skull table in their field of vision created by a short rostrum. The more anterior orbital placement generally would increase the field of vision, allowing them to maintain sight of their prey as long as possible on approach.

The more lateral orientation of the orbit increased the ability of the stereospondyl to be able to visualise prey in the water column. The Rhytidosteoidea, Trematosauroida and Brachyopoidea had species with the most pronounced lateral orientation. The lateral orientation in some Trematosauroida would support a piscivorous prey acquisition mode, they would be able to keep the prey in their field of vision (Grigg and Kirschner, 2015). The lateral orbits in Rhytidosteoidea would not discount a terrestrial mode of living, but it does support the semi-urophagous diet suggested by Maganuco et al., (2014). Being able to perceive prey through the depth of the water column could be a considerable advantage to seeking out slow moving, but swimming, prey, as seen in several species of extant amphibian and discussed in the comparative anatomy chapter (Chapter six). The eye position is important to the field of vision in and out of water.

The short and wide skulls of the Brachyopoidea would lend themselves to great resistance to strain (Anderson et al., 2013), add this to their laterally orientated orbits and it can be inferred that the Brachyopoidea also fed on hard shelled prey. The two *Plagiosuchus* species had wide and triangular subtemporal vacuities, allowing for more complex muscle groups to complement their short and wide skulls. From this it can be inferred that it is possible that *Plagiosuchus* and *Gerrothorax* had comparatively strong bites for the flattened skulls of stereospondyls. The Plagiosauridae have been imagined as benthic dwelling ambush predators because of the presence of a small process believed to be an attachment site for hyobranchial apparatus required for suction feeding (Damiani et al., 2009), a strong bite would be advantageous to subdue prey and prevent breakage (Anderson et al., 2013). Their skull shapes are more similar to those proposed by Taylor (1987) and Damiani (2001) to be capable of producing sufficient suction forces to catch aquatic prey leaving suction and ram feeding equally possible.

Although the tooth bearing ectopterygoid followed the narrowing/orientation change that was seen so frequently, the palatine did not. The palatine PC1 was the change of orientation, but PC2 showed a widening. The palatine was anterior to the ectopterygoid on the palate and sometime had an anteriorly widened head. Many of the species possessing a narrow ectopterygoid were from African deposits. The bone would not have

been especially strong, which may be some indication of the prey types that were available in Africa. Softer bodied or smaller items would be more suited to this weaker bone. Jeannot et al., (2006) suggested an insectivorous diet for some of the Early Triassic African species, which is consistent with the capabilities of the ectopterygoid. Due to the low numbers of preserved palatal elements of different species, it may be prudent not to attempt to infer much palaeobiology solely from these aspects but they may be used in conjunction with outer elements of anatomy to create a fuller picture of life history characteristics.

The subtemporal vacuities followed the same patterns in shape changes as most of the skeletal elements analysed here. Many of the stereospondyls with narrow STVs (such as Archegosauridae) were from the Permian. Narrow vacuities could limit the jaw motion of the species. There are differences in the muscle composition of the jaw closing musculature in extant amphibians, and the shape changes in the STV may reflect these so the shape of the subtemporal vacuity (fenestrae) is functionally informative (Yates, 1999; Damiani et al., 2009). Most stereospondyl skulls are stegokrotaphic, the mouth closing muscles were entirely underneath the skull roof, restricting the “margins of the mouth” (Damiani et al., 2009). A long and narrow STV would restrict the jaw muscle composition by restricting the space for muscle passage. The Brachyopoidea had narrowed subtemporal vacuities creating a direct up and down muscle action, coupled with a strong skull could create a clamp like fixture, though with the low species number, this is difficult to say this with certainty. The subtemporal vacuity is not heavily featured in character based phylogenies (Schoch, 2000; Warren and Marsicano, 2000; Warren et al., 2011), and given the overlap in morphospace, it should probably remain so or perhaps it needs more discrete states. The STV may provide some insight into the jaw closing function, but it is not taxonomically informative so it will be discussed in greater depth in the comparative anatomy chapter.

4.4.5 Conclusions

In response to the original hypotheses it can be said that several but not all stereospondyl taxonomic groups can be delimited from each other in morphospace by their skull roof and palatal anatomy. Nares and orbits correlate with the skull outline in dorsal view. Extant amphibian skull shapes can be delimited by groups and these groups show less variation in dorsal view than stereospondyls.

There are differences between some of the stereospondyl taxonomic groups in all of the aspects analysed here, so there may be functional differences associated with these shape changes. Many of the characteristics could not be categorised in the discrete / binary approach enforced on character state analyses. These results will be used as a platform for characterising the skulls at a taxonomic group level and the subsequent life history characteristics derived from comparative anatomy.

Chapter 5: Consensus shapes of stereospondyl skulls

5.1 Overview

The aim of this chapter is to provide a brief description of the shape and size of each group of stereospondyls and compare the findings to the descriptions of the groups in the literature. An interesting advantage of morphometric studies is that a consensus, or average, shape can be created from specimens when the Procrustes superimposition is carried out. Geometric morphometrics works on a continuous scale, whereas traditional character based morphometric studies do not allow for gradients, they are discrete states. A mean cannot be created from discrete states, but it can be created from scalable vectors, as used in geometric morphometrics. An additional benefit is to be able to create typical shapes for preassigned groups, which in this case is taxonomic groups of stereospondyls. For example, creating an average *Capitosauroides* moves away from the traditional species based paleobiology studies, and moves toward a group level understanding of the morphology, which, in addition to some basic size measurements, can then be used in finding the most appropriate analogues in comparative anatomy. Combining comparative anatomy with morphology and fossil record information can provide novel insight in to the rise and fall of the stereospondyls.

5.2 Skull measurements

Seven measurements were taken from stereospondyl skulls in dorsal view to provide an overall picture of stereospondyl size diversity to provide context. The measures that were taken encompass features that reflect assumed differences in skull shape between stereospondyls from different taxonomic groups. Here and in the consensus shape section the *Trematosauroides* have been split into two smaller groups as the inclusion of the metoposaurs resulted in such disparity in the previous chapter. Now the groups reflect the metoposaurs and the lonchoryforme trematosauroids (meaning long snouted, Schoch and Milner, 2000). Details of the measurements are in Table 5.1

A scale included in the original photograph was used to set the scale prior to measurement in ImageJ (Schneider et al., 2012). Linear features were recorded using the straight line and measure functions, whereas area measurements used the freehand tool. A

measurement of each variable was taken three times and the mean was used in the analyses.

Excepting orbit position and snout length, where metoposaur Trematosauroida and lonchoryforme Trematosauroida had the highest values respectively, the Capitosauroida had the highest values for each dimension. There was no single group that dominated the smallest values. These data show that the size diversity is as substantial as the shape diversity amongst stereospondyls. This brief summary is by no means intended to be an exhaustive analysis of stereospondyl size diversity, but as no summary of measurements is published elsewhere, it is useful to include it here. These data can contribute to the further study of stereospondyl skull dimensions and their impact on functional anatomy.

5.3 Consensus shapes

Coordinates from the discrete skull roof analysis were used to create a consensus shape for nine groups of stereospondyls based on the taxonomic groups. A data file was created for each of the nine groups with the species that were assigned to that group, ranging in number from three (Brachyopoidea) to 22 (Capitosauroida). Each of the files were imported in to MorphoJ (version 1.6d 2015) and subject to Procrustes superimposition which created and graphically represented the consensus shape and the species distribution around those shapes (Figure 5.1).

The graphical representations were imported in to the image manipulation program GIMP (version 2.8.16, 2015). A reconstruction of the consensus shape of each group of stereospondyls was created by connecting the landmarks of the skull outline, the orbits, nares and the pineal foramen. The image was then mirrored to create the complete picture (Figure 5.2).

Table 5.1 Skull measurements used in the present analysis, listed alphabetically. Red lines on images denote the measurement that was taken, blue lines show markers used to create a guide.

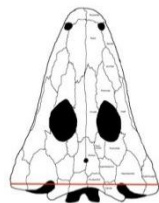
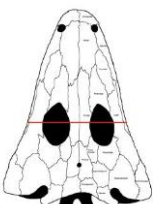
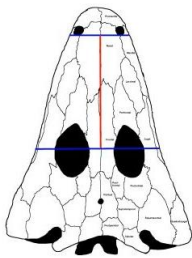
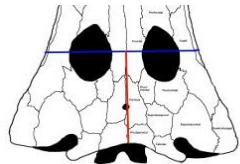
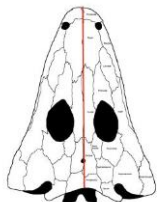
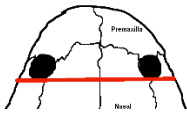
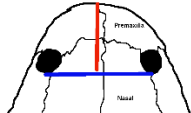
Measure	Description	Image
Maximum skull width (cm)	Distance between the lateral edges of the skull at its widest point.	
Mid orbital width (cm)	Width of the skull at the level of the mid orbit.	
Mid skull length (cm)	Distance from the level of the mid orbit to the level of the posterior nasal margin	
Orbit position (cm)	Distance from the back of skull to mid orbit	
Skull length (cm)	Anterior margin of the suture between the premaxillae to the posterior margin of the post parietals.	
Skull width at the nares (cm)	Width of the skull at the posterior margin of the nares	
Snout length (cm)	Posterior margin of the nares to the anterior margin of the skull table	

Table 5.2 Descriptive statistics for seven metrics of skull size and shape for nine taxonomic groups and stem stereospondyls. Species were only included where the relevant area was complete. Each measure is also illustrated in Table 5.1.

Taxonomic group		N	Mean	SE	SD	Min	Median	Maximum
Max Skull width (cm)	Archegosauridae	9	15.39	2.33	6.98	8.54	13.72	31.28
	Brachyopoidea	4	19.00	6.88	13.76	10.95	12.73	39.61
	Capitosauroidae	25	26.87	2.48	12.42	9.83	25.05	50.25
	Plagiosauroidae	2	28.92	2.52	3.56	26.4	28.92	31.44
	Rhinesuchidae	5	16.09	4.84	10.82	4.27	18.77	30.33
	Rhytidosteoidea	13	15.22	3.03	10.91	1.80	10.41	39.42
	Stem	5	14.59	2.33	5.22	8.73	12.59	21.33
	Trematosauroidae	12	13.20	4.76	16.49	1.11	10.90	28.07
	Metoposauroidae	7	22.42	6.23	16.49	2.71	17.03	17.50
Mid orbit Skull width (cm)	Archegosauridae	10	11.08	1.59	5.03	6.37	10.55	23.26
	Brachyopoidea	4	13.18	5.07	10.13	7.42	8.47	28.35
	Capitosauroidae	27	23.22	2.02	10.52	8.02	21.51	44.05
	Plagiosauroidae	2	19.58	4.68	6.62	14.9	19.58	24.26
	Rhinesuchidae	6	12.82	2.96	7.26	3.46	13.93	21.43
	Rhytidosteoidea	14	10.79	2.07	7.73	1.35	8.49	30.70
	Stem	5	11.28	1.95	4.35	6.98	9.54	16.01
	Trematosauroidae	13	8.27	2.59	9.36	3.09	6.23	15.74
	Metoposauroidae	7	13.79	3.54	9.37	1.81	10.36	26.94
Mid SL (cm)	Archegosauridae	6	10.54	1.96	4.81	2.57	10.74	16.08
	Brachyopoidea	3	2.66	0.58	1.00	1.69	2.60	3.69
	Capitosauroidae	19	20.07	2.16	9.43	5.20	19.94	41.32
	Plagiosauroidae	2	3.92	2.10	2.97	1.82	3.92	6.02
	Rhinesuchidae	4	12.01	3.83	7.65	1.65	14.05	18.31
	Rhytidosteoidea	11	4.41	0.72	2.38	0.57	4.13	8.52
	Stem	4	7.62	0.88	1.76	5.23	8.08	9.08
	Trematosauroidae	11	7.39	1.12	3.72	0.76	6.98	14.48
	Metoposauroidae	5	8.40	1.66	3.72	5.45	6.04	12.76

Table 5.2 Continued

Taxonomic group		N	Mean	SE	StDev	Min	Median	Maximum
Orbit position (cm)	Archegosauridae	8	8.28	0.52	1.47	6.37	8.51	10.44
	Brachyopoidea	3	5.65	0.77	1.34	4.80	4.96	7.19
	Capitosauroidae	26	10.49	0.95	4.86	3.67	9.24	21.81
	Plagiosauroidae	2	8.11	2.77	3.92	5.33	8.11	10.88
	Rhinesuchidae	6	7.33	1.64	4.01	2.10	8.38	11.49
	Rhytidosteoidea	12	6.99	1.36	4.71	0.82	4.98	16.51
	Stem	4	5.69	0.71	1.41	3.69	6.07	6.94
	Trematosauroidae	11	8.24	3.07	10.19	3.52	6.77	19.83
	Metoposauroidae	6	16.91	4.16	10.19	9.76	10.87	32.38
Skull length (cm)	Archegosauridae	6	26.63	4.08	9.99	13.69	26.41	37.81
	Brachyopoidea	3	9.617	0.33	0.571	8.96	9.89	10.00
	Capitosauroidae	19	33.69	3.49	15.22	11.12	30.03	67.47
	Plagiosauroidae	2	16.16	6.96	9.84	9.20	16.16	23.12
	Rhinesuchidae	4	23.76	6.51	13.03	4.74	29.01	32.29
	Rhytidosteoidea	13	13.77	2.32	8.36	1.77	10.72	28.25
	Stem	5	15.09	1.41	3.15	10.7	15.87	19.15
	Trematosauroidae	12	22.86	5.02	17.39	11.33	17.39	39.98
	Metoposauroidae	6	24.80	4.10	17.39	3.10	18.67	47.83
SW at nares (cm)	Archegosauridae	7	6.07	1.24	3.27	3.42	4.51	12.23
	Brachyopoidea	3	3.44	0.98	1.70	1.50	4.16	4.66
	Capitosauroidae	21	11.00	1.14	5.22	4.98	10.26	23.26
	Plagiosauroidae	2	8.06	1.37	1.94	6.69	8.06	9.44
	Rhinesuchidae	5	6.07	1.62	3.62	1.76	8.32	8.92
	Rhytidosteoidea	11	5.31	1.21	4.00	0.88	3.78	14.06
	Stem	5	7.95	2.11	4.71	3.97	5.36	15.02
	Trematosauroidae	12	3.98	1.74	6.01	1.14	3.38	10.81
	Metoposauroidae	5	10.52	2.68	6.01	4.83	7.03	17.15

Table 5.2 Continued

Taxonomic group		N	Mean	SE	StDev	Min	Median	Maximum
Snout length (cm)	Archegosauridae	6	5.83	1.31	3.20	2.12	5.31	9.70
	Brachyopoidea	3	0.99	0.29	0.50	0.43	1.14	1.40
	Capitosauroidae	20	4.61	0.36	1.63	2.25	4.31	7.17
	Plagiosauroidae	1	0.73	*	*	0.73	0.73	0.73
	Rhinesuchidae	5	2.09	0.63	1.41	0.45	2.41	3.69
	Rhytidosteoidea	12	1.70	0.90	1.02	0.36	1.78	3.19
	Stem	5	2.54	0.23	0.50	1.70	2.73	3.01
	Trematosauroidae	12	14.11	1.25	4.35	5.36	9.97	29.91
	Metoposauroidae	6	7.85	1.78	4.35	3.40	6.47	13.72

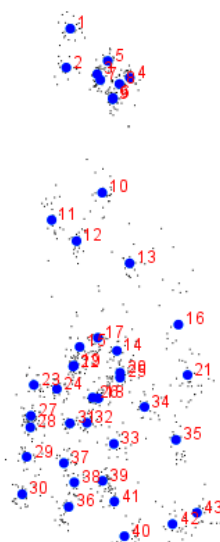


Figure 5.1 Consensus shape and species distribution of half of the skull of Capitosauroidae created by Procrustes superimposition of 42 discrete landmarks on 22 species as used in chapter four and described in Table 4.2.

The images did not include the positions of sutures as the aim was to include the most pertinent functional morphology that can be subsequently compared to extant species. The skull outline and position of the nares and orbits were the most directly comparable anatomical features.

The earliest stereospondyls that create the stem stereospondyl group had medium sized skulls with little variation in size (Table 5.2). Nares were positioned on the lateral skull margin, leaving a small amount of prenarial rostrum (Figure 5.2). Orbits were closer to the skull midline than the lateral margin and the overall skull shape was longer than wide, but only minimal rostral narrowing (Table 5.2, Figure 5.3). Their phylogeny is contested and the assignment of species to the Archegosauridae verses the stem group changes frequently (Schoch and Milner, 2000; Yates and Warren, 2000; Schoch, 2013; Maganuco et al., 2014). Stem stereospondyl skulls were described by Schoch and Milner (2000) as longitudinally parabolic with narrowed mid skull table and slit like squamosal embayments, though they also noted considerable variation in shape. The general shape was recovered in the present consensus shape, but the squamosal embayments were wider in this present study. Schoch and Milner's (2000) description was largely based on the genus *Sclerocephalus*. The group here did not include the genus *Sclerocephalus* which was included with the Archegosauridae as per Maganuco et al., (2014).

The Archegosauridae had longer but narrower skulls (mean skull length of 6 species cm \pm SE = 26.63 ± 4.08 , Table 5.2) than the earliest stereospondyls. Archegosauridae had the longest average snout length and were in the lower half of snout widths across all groups with (Table 5.2). Archegosauridae orbits aligned with the midline of the skull and occupied a large area of the skull at the orbit. The nares were orientated with the skull midline but position at the lateral margins of the skull. Schoch and Milner (2000) referred to the skull shape as having a width to length ratio as greater than 2.0, which has been retrieved here. The posterior skull margin is concave between the tabular horns, a character which was described by Witzmann (2006) for adults of *Archegosaurus dechini*, it was present sufficiently amongst this group to be retained in the consensus shape. Additionally the posterolateral corner of the skull is posterior to the tabular, a feature not previously focussed on in this group.

The lonchorynchine Trematosauroidae had narrower skulls than Archegosauridae and had particularly narrowed rostrums. Their orbits were smaller and had a lateral placement that did not reach the skull margin. The centre and posterolateral corners of the posterior skull margin were aligned and the tabular extended posteriorly. Schoch and Milner (2000) described the lonchorynchine trematosaurids as the most elaborate morphotype of the higher stereospondyls with elongated snouts and bottle shaped skulls. Their skulls were a medium length (Table 5.2) and the consensus shape supports Schoch and Milner's

(2000) description, though the extreme rostrum narrowing is tempered by the inclusion of less extreme genera such as *Angusarus*, *Trematolestes* and *Benthosuchus*.

Schoch and Milner (2000) described the Rhinesuchidae as having a deep otic notch, seen here, with parallel margins, which was not seen here. The term “deep” is an example of subjective language and its applications in palaeontology. Five of the seven known Rhinesuchidae species were included in creating the consensus shape. A brief inspection of the individual species (both the original specimens and those figured in Schoch and Milner 2000) shows that the consensus shape has otic notches that are representative of the species, and that the description of parallel used by Schoch and Milner (2000) does not apply to the entirety of the otic notch. The consensus shape had posteriorly extended tabulars as described in Schoch and Milner (2000). The tabulars were in line with the posterolateral corners of the skull table, the post parietals were well anterior. Rhinesuchidae had fairly large skulls that were 50% wider at the orbit than at the naris but their large size means that this does not give a narrowed rostrum (Table 5.2).

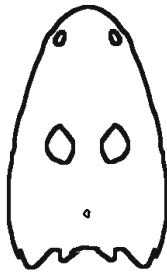
The Rhytidosteoidea had laterally positioned orbits, concurring with Schoch and Milner (2000). The skulls were small (Table 5.2). There was a large interorbital and internarial distance, a feature that has been described as characteristic of the Rhytidosteoidea (Dias da Silva and Marsicano, 2011). Their skulls were triangular, with gradual rather than sharp preorbital narrowing (as described by Dias da Silva and Marsicano, 2011) but this was not exclusive to the Rhytidosteoidea.

The Plagiosauroidae were few in number (to date three species have been fully described) but their morphology was very distinct. The consensus shape was only created from two of the three species (*Plagiosternum granulosum* was very fragmentary so could not be included) but illustrated the key features of the group as per Damiani et al., (2009). The skull was broader than it was long (Table 5.2, Figure 5.3), with orbits that were proportionally larger than any other group of stereospondyls, whilst the nares were comparably tiny. The posterior skull margin was almost flat, with no discernible otic notch.

The Brachyopoidea consensus shape showed a short parabolic skull with lateral orbits and nares. The Brachyopoidea of Jurassic and later Australia were not included in the measurements here because they lack complete skulls, but *Siderops kehli* was estimated to have had a skull in excess of 50cm (Warren and Hutchinson, 1983), the lower mandible of *Koolasuchus cleelandi* was a similar length (Warren et al., 1997).

Stem stereospondyls

(n = 4)



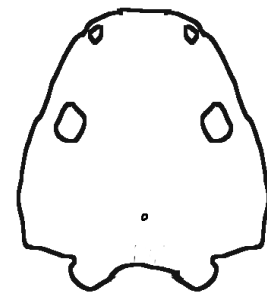
Rhinesuchidae

(n = 5)



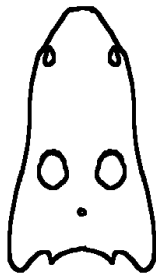
Brachyopoidea

(n = 3)



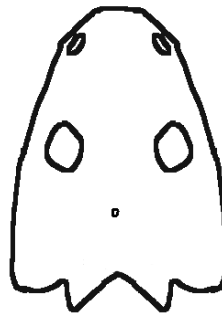
Archegosauridae

(n = 8)



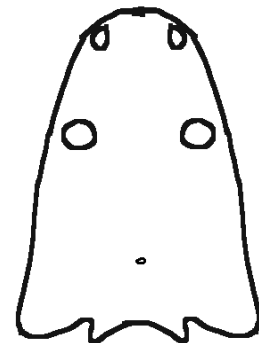
Rhytidosteoidea

(n = 17)



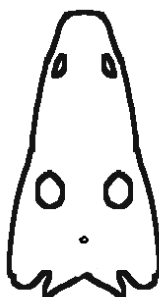
metoposaur Trematosauroida

(n = 4)



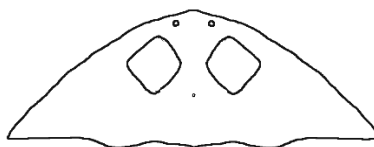
lonchorhynchine
Trematosauroida

(n = 14)



Plagiosauroida

(n = 2)



Capitosauroida

(n = 22)

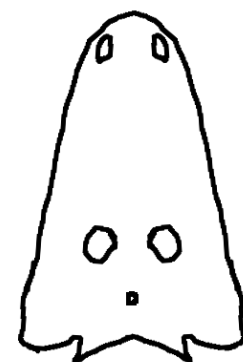


Figure 57

Figure 5.2 Consensus shape of stem stereospondyls created by Procrustes superimposition of 42 discrete landmarks on groups of stereospondyls

Warren and Marisicano (2000) did not include any dorsal skull roof or skull shape characteristics as exclusively Brachyopoidea traits though Damiani et al., (2003) described the skull as it is seen here, and with anteriorly placed orbits. What is considered an anteriorly placed orbit is subjective, but the consensus shape had orbits that were placed further anteriorly than most other groups. Their skulls were small (Table 5.2) but their orbit was still positioned at roughly half way down the skull table (as measured from the back of the skull (Tables 5.1 and 5.2). The tabulars formed clear projecting horns, but no otic notch, the remainder of the posterior skull margin was straight (Figure 5.2).

Schoch and Milner (2000) describe the metoposaur Trematosauroidae as having large and closely placed nares and laterally placed orbits. The consensus shape had laterally placed orbits that were in the anterior half of the skull table and the nares were large, but not particularly closely placed (Table 5.2). The size of the nares in individual species likely made them appear closely placed because of the anterior placement on the rostrum. The entire skull was broad, with only the slightest narrowing to the anterior margin of the skull. There were clear tabular horn projections with some concave curving between them. The posterolateral corners of the skull margin were not extended posteriorly beyond the tabulars though they did slightly exceed the posterior extent of the postparietals.

The Capitosauroidae were the largest of the stereospondyls (mean skull length of 19 species $33.69 \text{ cm} \pm 3.49$ Table 5.2) with some species reaching skull lengths in excess of 150cm (Schoch, 2000). Capitosauroidae orbits were close to the midline of the skull and well posterior in the skull table. The nares were large and laterally placed leaving a small amount of prenasal rostrum, all of which were features described by Schoch and Milner (2000). Schoch and Milner (2000) described the tabulars as being long and slender, which was also shown in the consensus shape. Excepting the tabular projection the posterior skull margin was straight between the postparietal posterior margin and the posterolateral corners.

Skull narrowing has occurred in both the Permian Archegosauridae and the lonchorhynchine Trematosauroidae. Laterally placed orbits can be seen both Trematosauroidae groups, as well as Brachyopoidea and Rhytidosteoidea, three of these four groups had relatively wide skulls. The Permian/Triassic Rhinesuchidae and the Triassic Capitosauroidae had medially placed orbits that were at the posterior of the skull table. Nares were typically at the lateral skull margin, but the prenasal rostrum varied in length, it was longest in groups with narrowed skulls.

The stereospondyl groups each display their own unique consensus shape, but several of those features overlap with other groups, as is the nature of related species. The consensus shapes, average sizes and the information from the taxonomic groups and fossil record will allow us to compare the stereospondyl with extant species in the next chapter to propose the most likely life history characteristics for them as detailed in the next chapter.

Chapter 6: Comparative Anatomy of Stereospondyls

The present chapter reviews the use of comparative anatomy in the stereospondyl literature followed by an overview of stereospondyl anatomy alongside extant amphibians and reptiles. Stereospondyl skull roof and palate anatomy was presented in chapter two and the gross anatomy are not repeated here but additional detail on dentition, the mandible and post cranial anatomy are presented.

6.1 Comparative anatomy in stereospondyl literature

The life histories of fossils have long been inferred from comparison with extant species. Stereospondyls are frequently described as “crocodiliform” due to their large and heavily ossified skulls (Schoch and Milner, 2000; Yates and Warren, 2000; Fortuny et al., 2011). When stereospondyls are compared with amphibians it is commonly done by comparing the body plan (Witzmann and Schoch, 2006; Sanchez et al., 2010) or larval development (Schoch, 2006; Witzmann, 2006; Damiani et al., 2009) with urodeles. Occasionally fish are used as references for general anatomy such as muscle arrangement (Damiani et al., 2009; Witzmann, 2007; Schoch et al., 2014). Many authors have highlighted that there are more differences than similarities between early and extant amphibians (e.g. Schoch and Milner, 2000; Wells, 2007; Vitt and Caldwell, 2014; Fortuny et al., 2016).

Despite substantial morphological variation in stereospondyl skull shape, comparisons between stereospondyls and extant species rarely go into much depth beyond “gharial” (see Schoch and Milner, 2000; Steyer, 2002; Witzmann, 2006). The gharial shape (Figure 6.1) is commonly used to infer an active swimming and piscivorous life style (Steyer, 2002; Witzmann, 2005; Stayton and Ruta, 2006; Witzmann and Schoch 2006; Fortuny et al., 2011). Witzmann (2006) observed that long and flat snouts are also associated with lateral head swipes to catch prey, seen in long snouted crocodiles, gharials, the fish genus *Lepisosteus*, and river dolphins. Fortuny et al. (2011) made a similar observation about narrow snouted aquatic predators in general. Lateral head swiping comparisons are not limited to aquatic extant species, they were speculated for the capitosaur *Eocyclotosaurus appetolatus* based on a comparison with the urodele Tiger salamander (*Ambystoma tigrinum*) and their shared feature of very short necks, making side swiping head action the fastest method prey acquisition (Rinehart et al., 2015). The terrestrial salamander has a much shorter and blunter skull shape than the stereospondyl. The head swiping may be

the most likely action but the Tiger is salamander much smaller (snout vent length 15cm) than *E. appetolatus* (skull length 42.7 cm Rhinehart et al., 2015) evidencing that head swiping should be considered for more than the lonchorhynchine Trematosauroida.



Figure 6.1 Three narrow snouted species used in stereospondyl comparative anatomy, top the Amazon River Dolphin (*Inia geoffrensis*), middle the short nosed gar (*Lepisosteus plasostomu*) bottom, the gharial (*Gavialis gangeticus*)

The larger metoposaurs and capitosaurians have been generically compared to crocodiles (e.g. Fortuny et al., 2017). Broad snouted crocodiles have been used to speculate prey size differences between narrow and wide snouted stereospondyls, with the latter able to feed on larger prey as seen in these crocodiles (Witzmann and Scholz, 2007). However, given the skull shape variation in crocodile species (Pierce et al., 2008) and stereospondyl species (as evidenced in chapter four), this is far from an exhaustive comparison. Life history characteristics are not always inferred from extant species comparisons. Schoch (1999) identified the clear crocodile resemblance but proposed that the urodele *Amphiuma tridactylum* skull was similar to the capitosaur *Mastodonsaurus giganteus*, and the Japanese giant salamander *Andrias japonicus* was similar in body plan. The comparisons ended at shape and the extant species were not used to draw any life history conclusions. Perhaps it was the substantial size difference between *M. giganteus* and all extant skulls, *M. giganteus* had a total body length of 6 metres, which prevented Schoch (1999) from drawing any specific conclusions about the stereospondyl from the urodeles. The physical demands placed on *M. giganteus* would be substantially different from even the largest extant salamanders. Their mass would change metabolic demand (Kingsolver and Huey, 2008) and the greater weight would alter their movement capabilities. Accurately inferring movement from fossils requires substantial engineering techniques and specialist knowledge that was not the focus of the Schoch (1999) paper.

A small number of studies have gone into more depth in comparing stereospondyls to extant species. Fortuny et al. (2016) used FEA to compare amphibian and alligator bite properties with stereospondyls in multiple scenarios and found that the stereospondyl skulls showed more similar patterns of stress distribution to alligators over amphibians, which was attributed to the ossified skull roof of the former. Ultimately the alligator skull roof showed overall lower stress deformation than stereospondyl and extant amphibians, though stereospondyls had much lower stress deformation values in all cases than extant amphibians (Fortuny et al., 2016) which was also true for the palates (Lautenschlager et al., 2016). The take home message from these unique analysis was that stereospondyls occupied a variety of niches that differed from both extant amphibians and crocodilians, the “best case scenario”, based on deformations, was a powerful direct bite favoured over unilateral bites or suction feeding. Though these studies undeniably contributed substantial insight into the bite performance of stereospondyls they considered only two species and only one element of prey acquisition and should be expanded to include more species and groups. The studies exclusively focussed on biting, the process of sighting

and catching prey was not taken into account, and this can be considered through the comparison of extant amphibians and reptiles.

Schoch et al. (2014) used amphibian and fish eyes as a basis for their examination of orbits and potential eye types (large spherical eyes filling the orbits, small eyes in large orbits and flattened eyeballs) to estimate the most likely eye size for Plagiosauroidae. The authors suggested an amphibian-like eyeball (small eye in a large socket) anteriorly positioned in the orbit which was substantially smaller than the orbit was most likely (Schoch et al., 2014). Maganuco et al. (2014) also suggested extant amphibian type eyes for Rhytidosteoidea, though the authors considered the eye to be large and bulging based on the volume of the orbital cavity. Large interpterygoid vacuities (interpterygoid vacuities are illustrated in chapter 2, methods) in *Archegosaurus dechini* were inferred to facilitate eye retraction, a conclusion drawn when the palate was compared to extant urodeles and anurans (Witzmann, 2006). Stereospondyl literature concurs that stereospondyls likely had the same eye as extant amphibians and although orbit position is considered a defining taxonomic feature (Schoch and Milner, 2000) it has only once been considered in comparative anatomy. Fortuny et al. (2017) proposed that the anterior orbit position seen in metoposaurs may be used in a similar way to turtles and crocodiles who raise the eyes above the water line to look for predators and prey. Considering the range of stereospondyl orbit positions demonstrated in chapter 4 this warrants further comparisons with extant species to consider the extent to which it can impact an individual's life history.

In addition to prey seeking behaviour, more life history characteristics have been suggested on the basis of comparisons with extant species, Witzmann (2006) speculated that the lack of gills in adult *A. dechini* did not infer a terrestrial mode of life, but that the species likely swam to the surface to gulp air, as seen in lungfishes and aquatic urodeles. Crocodiles and urodele swimming modalities were proposed for adult and juvenile *A. dechini* based on similarities in body plan and stiff and mobile trunks respectively (Witzmann and Schoch, 2006).

As with many other elements of stereospondyl biology, there is no widespread analysis of their comparative anatomy across the taxonomic groups, the studies highlighted above typically focus on fewer than three species at a time. Resource use (such as prey acquisition) can often be linked to differences in morphology of cranial and post cranial elements between potential competitors (Herrel et al., 2002). Given that stereospondyls have been shown to have substantial skull diversity and varied orbit placements, a review

of extant analogues could provide insights in to their life histories and so their evolutionary success as is carried out here.

6.2 Stereospondyl anatomy

Stereospondyl skulls were akinetic (Schoch, 2002) because interdigitating sutures are present throughout, meaning that the skull has little flexibility in the adult forms (Jaslow, 1990; Schoch and Milner, 2000). The lamellae between bone sutures prevented stress from torsion across the skull (Kathe, 1999).

Three muscles have been described for jaw closing action in stereospondyls, based on the jaw closing action of primitive salamandrids and some fish (Carroll and Holmes, 1980; Schoch et al., 2014). The adductor mandibulae internus passed from the dermal skull through the subtemporal vacuity and attached to the mandible and so the insertion was limited by the area available for the passage through the subtemporal vacuity (Carroll and Holmes, 1980). The adductor mandibulae externus muscle would have originated between the orbit and otic notch, it was limited anteriorly by the posterior tooth row and the anterior margin of the vacuity and laterally by the cheek (the area lateral to the orbit, Carroll and Holmes, 1980). Finally the adductor mandibulae posterior would have inserted in to the meckelian fossa on the mandible and been contained in the skull by the quadrate ramus of the pterygoid, the otic notch and the other mandibular muscles (i.e. the adductor mandibulae externus and adductor mandibulae internus).

The ectopterygoid, palatine and vomer were tooth bearing, creating a second toothrow in addition to the premaxillary and maxillary teeth. In addition to these teeth several species of stereospondyls had fangs on their vomers and at the anterior extent of their palatines and less frequently on the ectopterygoid (Figure 6.2). The large pterygoid supported the quadrate articulation and connect the basicranium (centre of the braincase) with the tooth rows. The basicranium was formed by the pterygoid and parasphenoid.

The occiput and occipital condyle showed some variation through the temnospondyls. In the primitive condition the medial basioccipital formed a single condyle which was surrounded by paired exoccipitals. The exoccipitals sutured dorsally with the postparietals and were connected to the tabulars by a pair of opisthotic ossifications (See Figure 6.3). The exoccipital had two process that are visible from the posterior view of the skull, four more are contained within the brain case. The vertical column is dorsally

directed and connects with the postparietals, and the large bilobed or paired condyles that project posteriorly for articulation with the atlas.

There were nine dermal bones in the stereospondyl mandible (Figure 6.4). The dentary, angular, glenoid and surangular were all visible on the labial side. The angular, the anterior portion of the dentary and the posterior projection of the surangular were also visible on the lingual surface along with the articular, prearticular (often forming a hameate process), splenial, postsplenial and the coronoid complex. All stereospondyls had a meckelian window on the lingual surface and an adductor window on the dorsal surface. Most stereospondyls had a post glenoid area but its size and shape varies (Warren and Black, 1985). The dentary was tooth bearing, and in some species some or all of the coronoid series had small teeth. One or two pairs of symphyseal fangs may be present in the highly plastic symphyseal region.

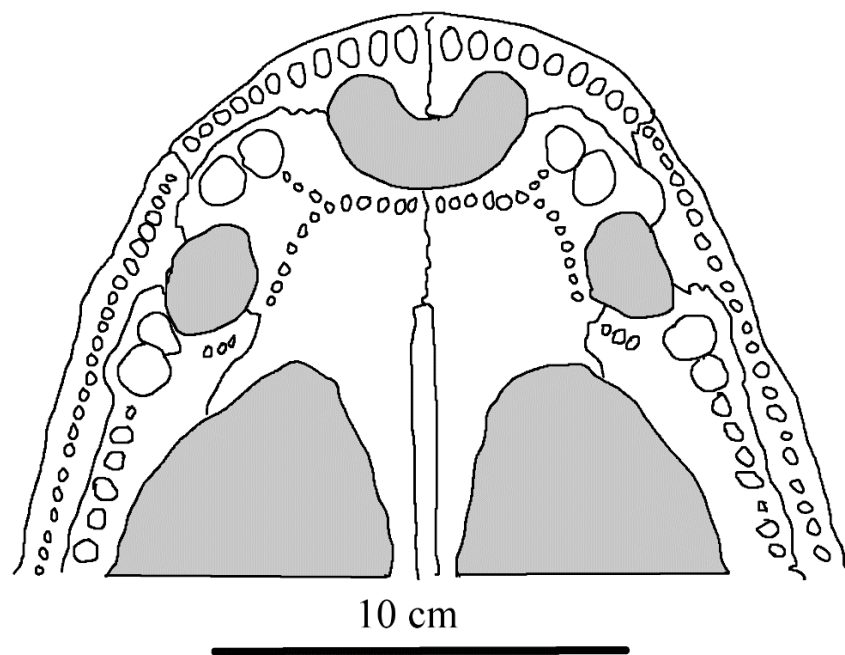


Figure 6.2 Typical dentition of stereospondyls in the palate of *Cyclotosaurus robustus* adapted from Schoch and Milner (2000). The palatine and vomers each had a pair of fangs.

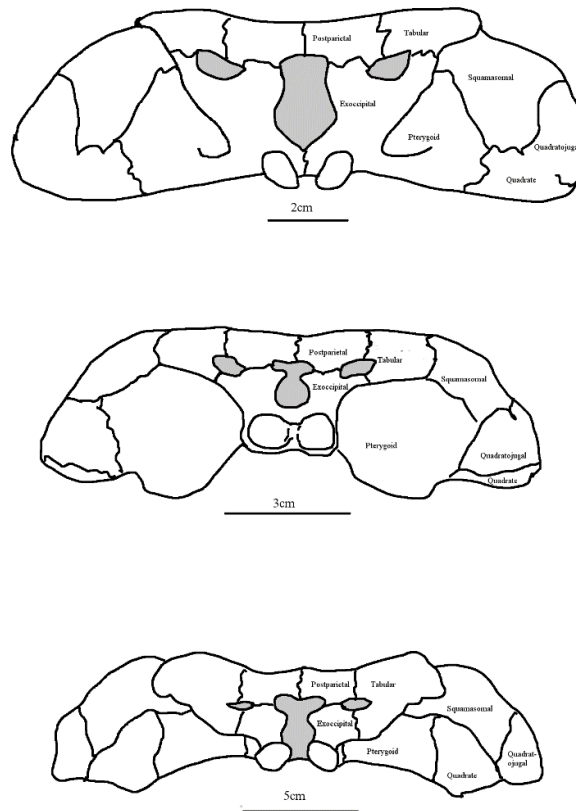


Figure 6.3 Occiput of stereospondyls top *Callistomordax kugleri* (adapted from Schoch 2008) middle *Konzukovia vestusa* (adapted from Schoch and Milner, 2000) bottom *Parotosuchus haughtoni* (adapted from Damiani 2001)

Stereospondyl vertebrae were made up of disc-like intercentrum and pleurocentra and neural arches (Figure 6.5). The number of vertebrae varies from 20-30 presacral vertebrae with two sacral vertebrae. The precise number of caudal vertebrae is unknown as no complete series has been found, though some species have had around 20 caudal vertebrae associated with their fossils. All trunk vertebrae except for the proatlas and atlas had dorsal ribs which varied in size and shape between stereospondyl species. Both broad and thin uncinate process have been found on stereospondyl ribs, which were particularly common amongst larger species. Sacral and caudal ribs can vary from rod like structures to flat and distally broadened (Figure 6.6).

The dermal portion of the pectoral girdles had the same distinctive pattern as the skull roof bones. A single interclavicle was bordered by paired clavicles and cleithra, though the latter is rarely found with fossils. The scapulocoracoids made up the endochronal point. The interclavicle could have an anteriorly narrowed point, but its body is often as wide as the skull (Figure 6.6).

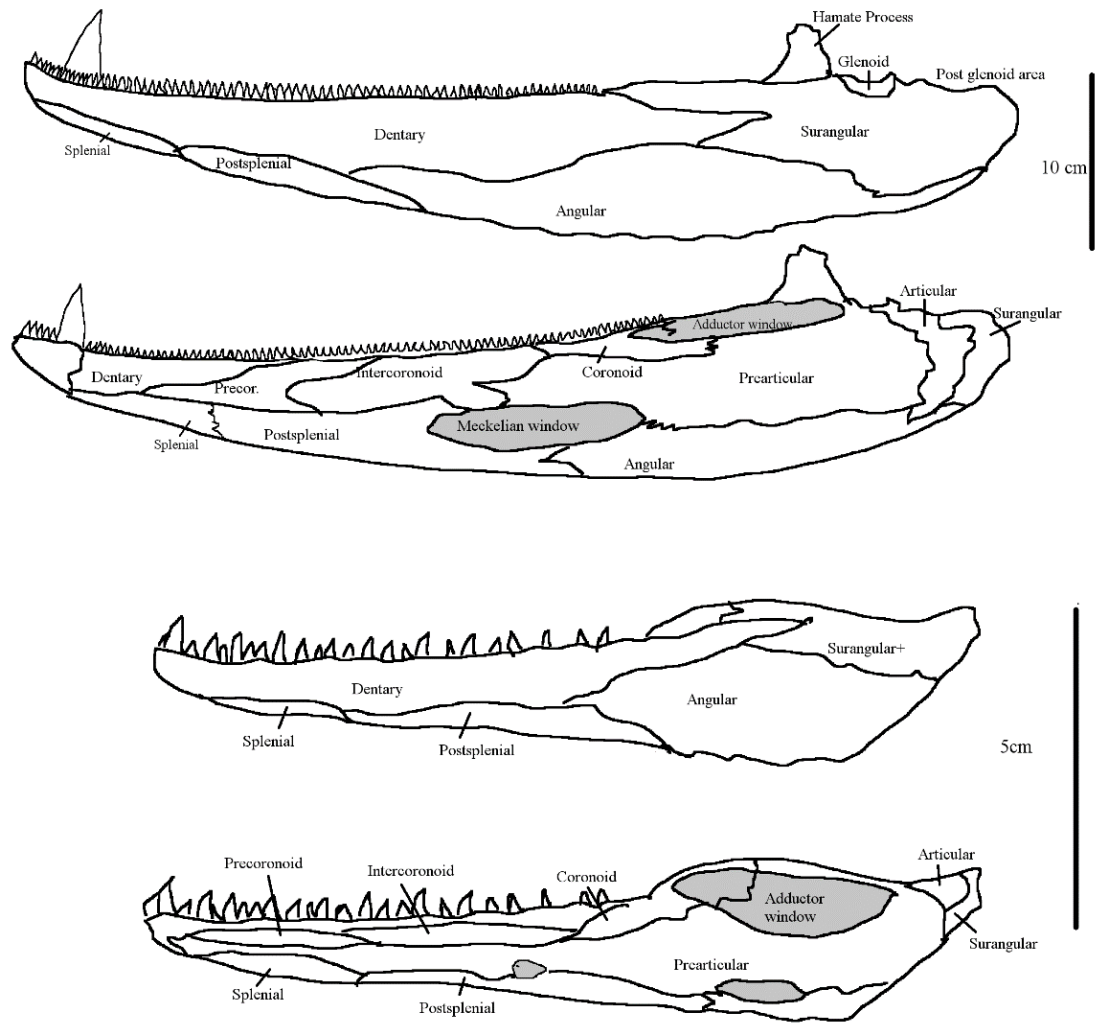


Figure 6.4 Mandibles of stereospondyls Top *Mastodonsaurus giganteus* labial and lingual views (drawn from author's own images) bottom *Scelerocephalus haseuri* labial and lingual views (adapted from Schoch and Witzmann 2009)

The humerus was simplistic in structure, some species had a poorly developed supinator process and epicondyles. The ulna and radius were usually shorter than the humerus with a short olecranon process. The normal pharyngeal formula was 2-2-3-3-3 with carpals remaining unossified. Paired ilia, ischia and a frequently unossified pubes made up the pelvic girdle. The ilium was more commonly identified than the other components, its dorsal component was a straight or slightly curved rod with a posterodorsal orientation. The femur had a distinct shaft with a medially raised head and obvious distal condyles. The tibia and fibula were small and the tarsus usually remained unossified with a pharyngeal formula of 2-2-3-4-3.

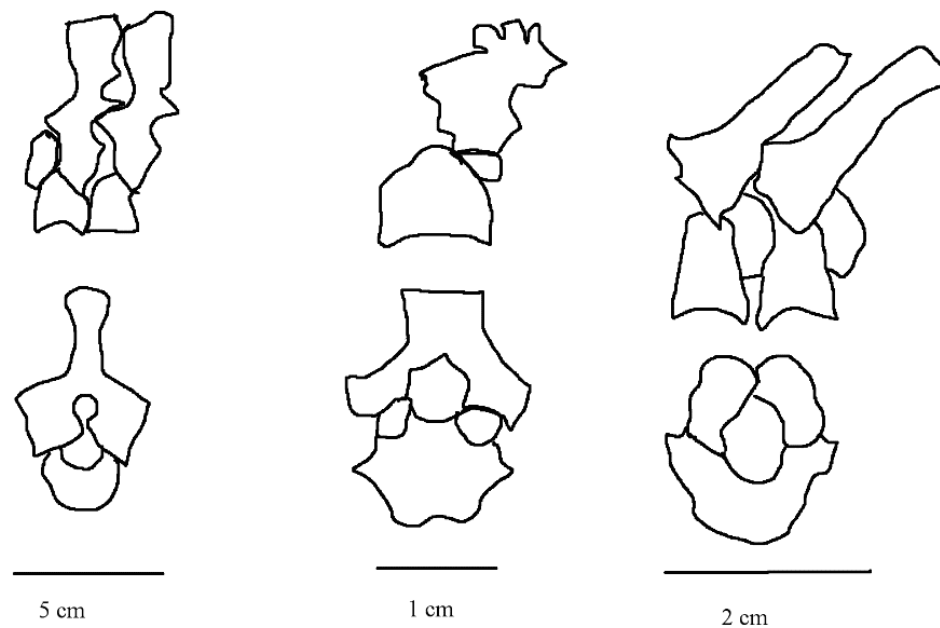


Figure 6.5 Vertebrae in lateral (top) and posterior (bottom) perspectives showing the variation in intercentra and neural arches. Left, *Sclerocephalus haseuri* (from Schoch and Witzmann 2009) centre *Laidlaria gracilis* (Warren 1998) right *Trematolestes hagdorni* (Schoch 2006)

Hypotheses

This chapter will aim to demonstrate that the variety of stereospondyl lifestyles can be inferred from their skull shapes and orbital position.

H1: Narrow and long preorbital areas are indicative of piscivorous diets

H2: Wider snouts are indicative of being able to take larger prey

H3: Lateral orbital placement is associated with terrestrial and deep aquatic species, not surface dwelling

H4: Centrally located orbits are associated with surface dwelling ambush predators

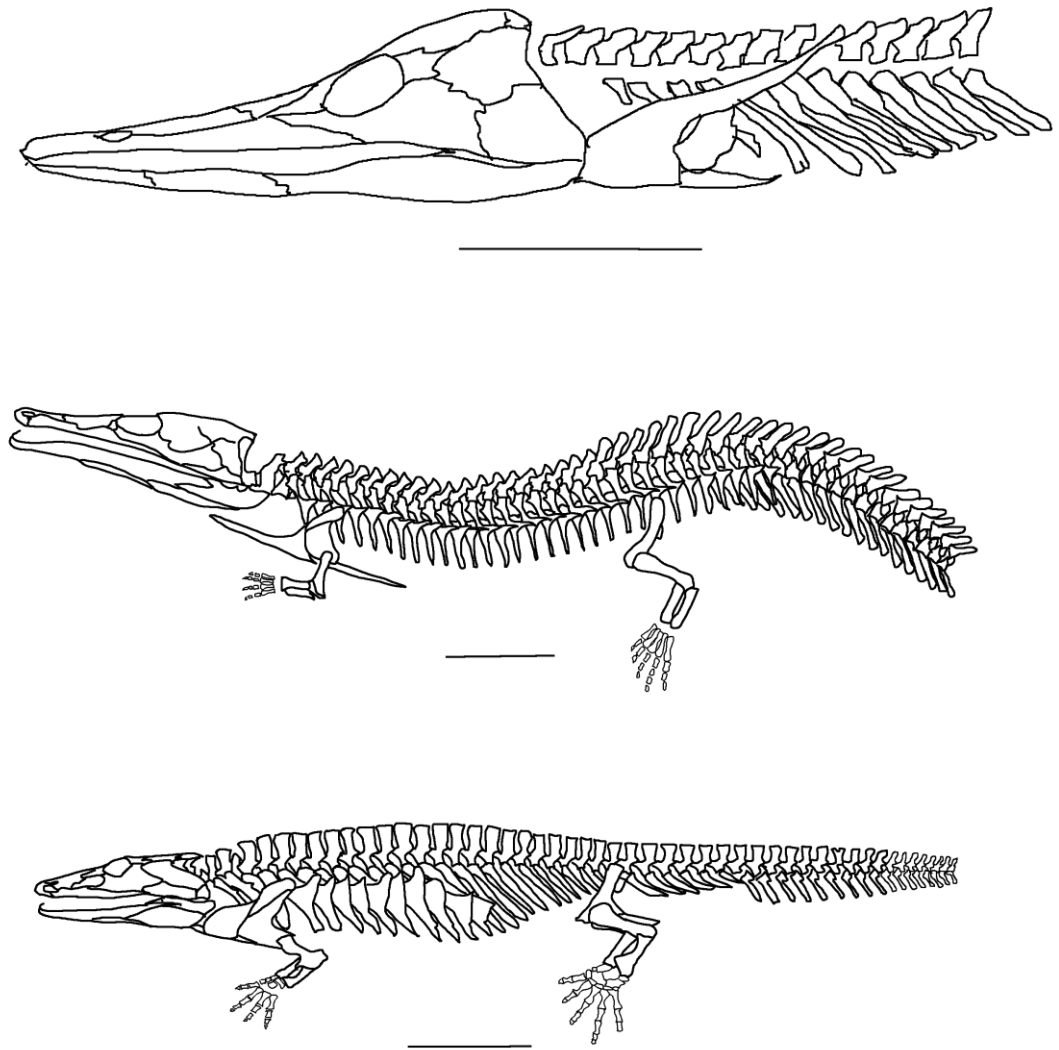


Figure 6.6 The skeleton Top, *Wantzonosaurus elongatus* (Steyer 2002), middle *Trematolestes hagdorni* (Schoch 2006), bottom *Sclecocephalus hasueri* (Schoch and Witzmann 2009) scale bars = 50 mm. Rib morphology varied between stereospondyl species. The pectoral girdle consisted of the clavicles, scapulocoracoid and interclavicle.

6.3 Amphibian and Reptilian Anatomy

Stereospondyl amphibian skulls differed quite substantially in bone composition from extant amphibians (Carroll and Holmes, 1980; Wells, 2007; Figure 6.8). Lineage dating inferred from molecular data suggest that extant lissamphibia did not descend from temnospondyls (Marjanovic and Laurin, 2007) which is supported by their morphological disparities. Though some authors may debate this (see Schoch and Milner, 2004). The skull table is greatly simplified in extant amphibians and many of the bones are never

ossified. Many of the post orbital skull bones seen in stereospondyls are absent entirely. Anurans and urodeles have weakly ossified skulls and mandibles, though caecilians possess a strongly ossified cranium it is much taller than the stereospondyl skull (Nishikawa and Schwenk, 2002). The braincase forms a structural beam, extending from the occiput to the snout in extant amphibians supporting the cheek and pterygoid, whereas it was suspended as an endochondral braincase in stereospondyls and other early amphibians (Carroll and Holmes, 1980). The size differences between stereospondyls and extant amphibians is vast, and the small size of the extant skulls is likely a key feature of the structural difference (Carroll and Holmes, 1980) though there is a generally flattening of skulls amongst the largest extant amphibians (Schoch, 1999). The main similarities between extant amphibians and stereospondyls are the presence of a toothed maxilla which occupies much of the lateral skull margin. The frontal and parietal complex is more variable in extant amphibians than stereospondyl amphibians (see figure 6.7-6.8). The palate is also very different between extant amphibians and stereospondyl amphibians (figure 6.8). The premaxilla and maxilla form the main tooth bearing region and are sutured on the palate, in congruence with stereospondyls but the ectopterygoid is absent and the palatine is only occasionally seen in anurans. Anurans have a larger gape than urodeles as the quadrate is usually at the posterior margin of the skull (Carroll and Holmes, 1980), a feature seen in stereospondyls. The Giant salamanders have paired and sutured vomers, as seen in stereospondyls, though there is no continuous connection of bones on the lateral margin of the palate in urodeles which is achieved in stereospondyls (see earlier discussion). Some anuran species have a long maxilla that extends the length of the palate. In extant amphibians the squamosal contacts the parietal without the intervention of the tabulars and supratemporal (Carroll and Holmes, 1980).

The jaw closing mechanisms of anurans and urodeles is likely to have evolved separately, based on the differences in skull morphology between the extant groups and Palaeozoic amphibians, (Carroll and Holmes, 1980). The much smaller size of extant amphibians means that the muscles will be greatly constrained by orbits and otic notches. In urodeles the adductor mandibular externus is always large, but it is often absent or reduced in anurans. The adductor mandibulae posterior is the most important jaw closing muscle in anurans but conversely is often absent or reduced in urodeles (Carroll and Holmes, 1980). The adductor mandibulae internalis is large in urodeles and less developed in anurans. Despite these differences, both groups have large muscle groups originating at the otic capsule. The muscle and bone morphology have led to differences in bite mechanics. The

Chinese Giant Salamander exhibits lowest stress values when prey are grasped at the anterior of the mouth (Fortuny et al., 2016), as determined by FEA. This FEA type study is lacking in anurans but they are generally described as using their tongue, suction feeding or forelimbs to immediately position prey at the back of their mouth, compensating for their generally weak jaws (Wells, 2007). Caecilian jaw action is much slower but more powerful than anuran and urodeles (Nishikawa and Schwenk, 2002).

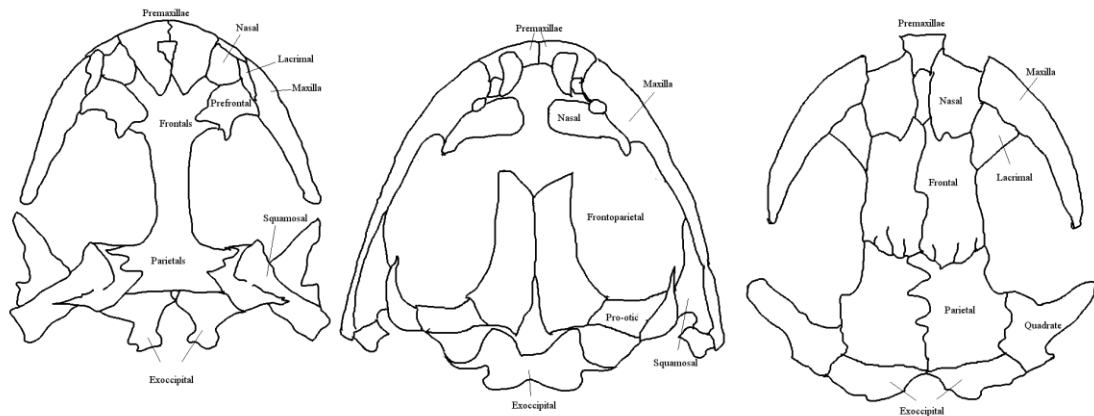


Figure 6.7 Extant amphibian skulls in dorsal aspect, left to right *Dicamptodon ensatus* (Pacific Giant Salamander – adapted from the digimorph project), *Rana temporaria* (Common frog adapted from Reynolds et al., 1913) and *Molge cristata* (Great Crested Newt adapted from Reynolds et al., 1913).

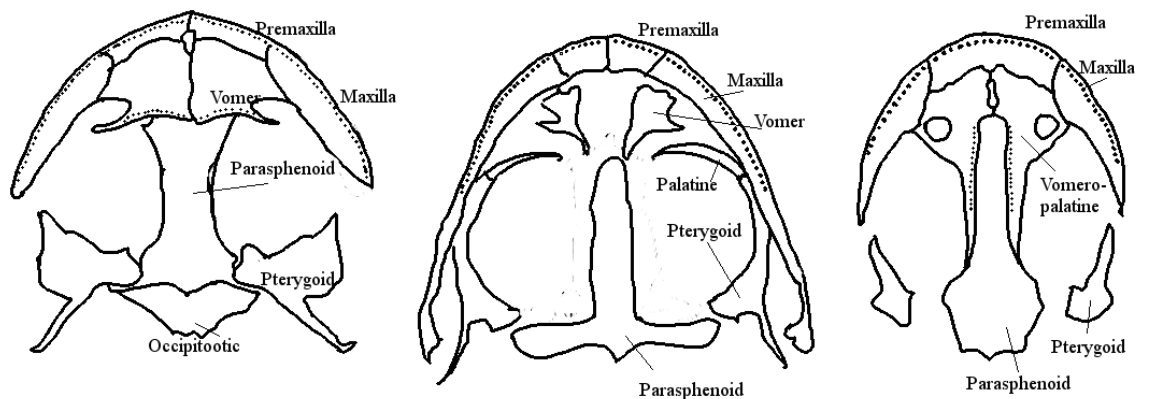


Figure 6.8 Extant amphibian skulls in ventral aspect, left to right *Dicamptodon ensatus* (Pacific Giant Salamander – adapted from the digimorph project), *Rana temporaria* (Common frog adapted from Reynolds et al., 1913) and *Molge cristata* (Great Crested Newt adapted from Reynolds et al., 1913).

Superficially stereospondyl skulls appeared more similar to extant crocodilians both in shape and skull bone composition (presence and shape of bones). In addition to the bones shared with amphibians, crocodilians and stereospondyls also shared a postorbital, prefrontal and jugal. However the nares in crocodilians often form a single fenestra and crocodilians have an additional pair of supratemporal fenestra. The quadrate and quadratojugal are not part of a continuous skull table as in stereospondyls, but are recessed in to the skull table (Figure 6.9).

The crocodilians have a secondary palate with internal nares whereas stereospondyls had an open palate with choanae (Figure 6.10). The secondary palate will add strength in bending and torsion so it cannot be assumed that the stereospondyl skull is exactly as strong. Both share palatines and ectopterygoids though the palatine has a central position in the palate in crocodilians. Stereospondyls and crocodilians shared palatal vacuities but the vacuities in the latter are much smaller. Crocodilians lack a parasphenoid and vomers but the overall anatomy is more similar than stereospondyls than the palates of extant amphibians. Crocodilians have the same three jaw closing muscles that were suspected to be present in early tetrapods and the muscles attach to the ventral surface of the skull and attach in the lower jaw (for specific details see Bona and Desojo, 2011) though crocodilians have a highly pinnate structure allowing for many internal tendons.

Crocodilians and stereospondyls are additionally similar in the relative heights of their skulls. Crocodilians, which are known to have some of the strongest recorded bite forces amongst vertebrates, do not follow the typical pattern of increased skull height to increase bite force seen amongst vertebrates such as hyenas and tegu lizards (Sellers et al., 2017). Throughout crocodilian evolution the move to platyrostry (flattened rostrums) has been in adaptation to an aquatic ambush mode of prey acquisition while increased adductor muscle mass has maintained high bite forces (Sellers et al., 2017).

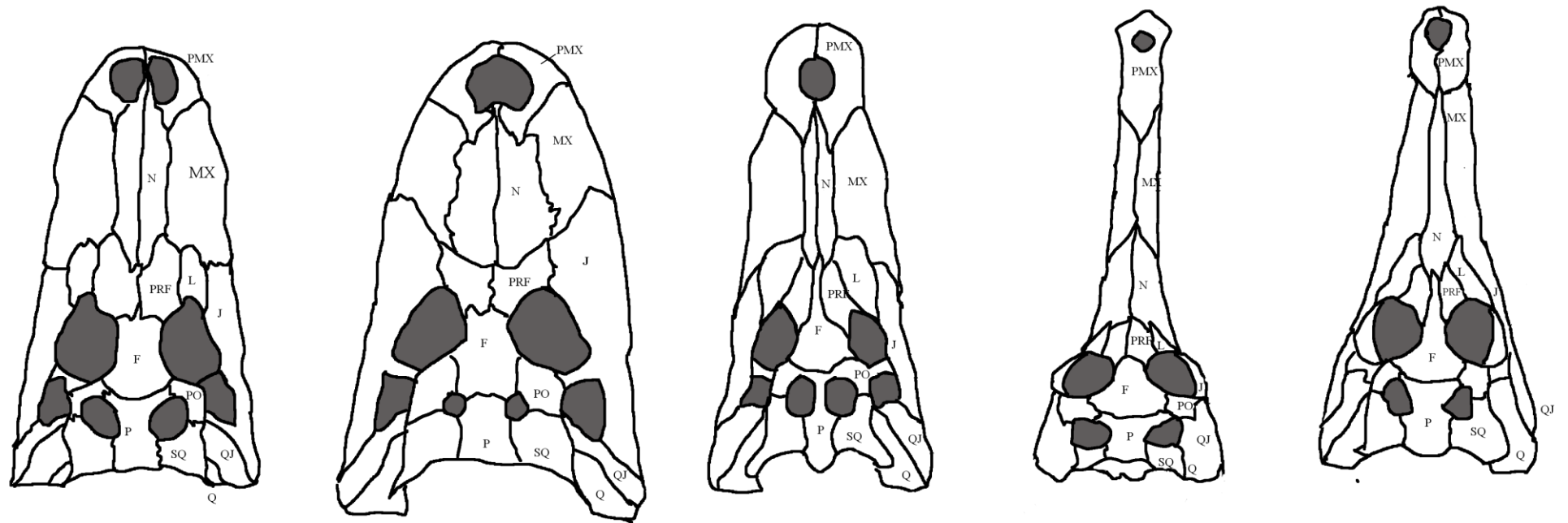


Figure 6.9 Extant crocodiliform skulls in dorsal aspect left to right *Alligator mississippiensis*, *Caimen yacare*, *Crocodylus niloticus*, *Gavialis gangeticus* and *Crocodylus johnstoni* adapted from the digimorph project. Abbreviations are as follows: PMX – premaxilla, MX – maxilla, N – nasal, L – lacrimal, PRF – prefrontal, L – lacrimal, J – jugal, PO – post orbital, F – frontal, P – parietal, SQ- squamosal, QJ – quadratojugal, Q - quadrate

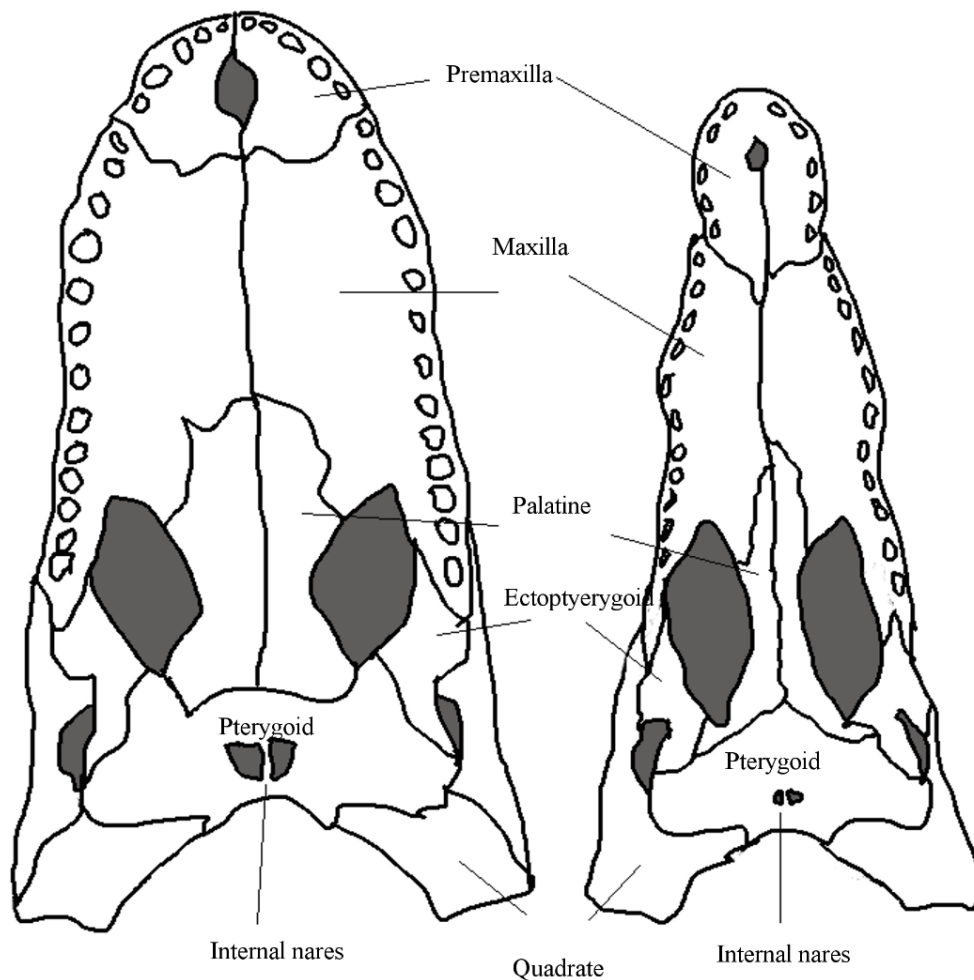


Figure 6.10 Extant crocodiliform skulls in ventral aspect left, *Alligator mississippiensis*, right, *Crocodylud porosus* adapted from the digimorph project

On the whole reptile diets are more diverse than amphibians as they include invertebrates, eggs and plant material described in addition to carnivory (Nishukawa and Schwenk, 2002) whereas amphibians are largely carnivorous and insectivorous (Wells, 2007). Crocodilians are fully carnivorous and capable of taking large prey such as marine turtles (Sellers et al., 2017) and zebra (Nishukawa and Schwenk, 2002). Crocodilians use a rapid head swipe to capture prey, and some turtle species also use forward and lateral strikes in ambush and active predation (Nishukawa and Schwenk, 2002). Jaws are used for capturing large prey and tongues are used for herbivory and insectivory (Nishukawa and Schwenk, 2002).

Dentition and tongues

In most stereospondyls the teeth of the lower jaw were oval, and compressed in mediolateral orientation (Sues and Schoch, 2013), their teeth were similar to osteichthyan fish (Maganuco, et al., 2014). Teeth that are oval and circular in cross section have been allied with a feeding action involving piercing and grabbing in extinct amphibians (Maganuco and Pasini, 2009) and other carnivores (Evans et al., 2007). Stereospondyls were widely believed to be piscivorous, due to the presence of slender spiked teeth in the anterior part of their mouths (Schoch and Milner, 2000), unfortunately, this assertion largely ignores the rest of the factors that influence prey acquisition. It is important to note that many fossils only have tooth bases, and not the teeth and so the data that could be inferred is limited. Rinehart et al. (2015) had success determining bite scenarios for *E. appelatus* from the tooth height and strength, but unfortunately this is not possible for many stereospondyls so we must look to extant comparisons for anatomy.

Extant amphibians have bicuspid or pedicellate teeth which are capable of a jointed movement. Stereospondyls often had large tusks or fangs which are rare in extant amphibians but more common in reptiles. Stereospondyl teeth are labyrinthodont with complex infolding of the dentine and enamel (Rinehart and Lucas, 2013). Teeth were conservative across temnospondyls and lacked roots and sockets, instead they were attached to the palatal bones by cementum (Rinehart and Lucas, 2013). Most anurans lack any dentition on their lower jaw and fangs only exist in four families, ranids, myobatrachids, leptodactylids and hylids, totalling roughly 30 species (as defined by Fabrezi and Emerson, 2003). Fangs are associated with large prey and aggressive biting behaviour, particularly in those species with non pedicellate teeth (Fabrezi and Emerson, 2003). Teeth act like cantilevered beams, free standing at one end and rigidly attached at the other, so their shape is essential to their function, for instance if tooth taper is long and slender it is well adapted for penetration but at greater risk of breakage. The opposite is true with less tapered teeth which are stronger but penetrate poorly (Rinehart and Lucas, 2013). Tooth shape can provide some insight into prey preference in extant amphibians and reptiles, broad and sturdy teeth indicate molluscs are part of the diet, and teeth capable of shearing indicate herbivory in reptiles, such as iguanas that have small and serrated teeth (Vitt and Caldwell, 2014). Considering the lack of shearing teeth in stereospondyls herbivory is not likely for stereospondyls.

The stereospondyl type conical fang teeth are more common in carnivorous bony fish and reptiles like crocodilians, but as with fanged amphibians they are associated with grabbing and holding prey.

The tongue is an important part of prey capture and processing in extant amphibians and varies considerably between groups (Nishikawa and Schwenk, 2002). The protruding tongue is a common prey capture method in terrestrial amphibians but it is largely useless in aquatic environments (Deban et al., 2001; Wells 2007; Vitt and Caldwell, 2014). Tongues also play a role in prey capture in some turtles and lizards with protrusion to contact prey but also as a lure (alligator snapping turtle) and chemoreception (squamates and some lizards) (Nishikawa and Schwenk, 2002). The presence of a tongue in temnospondyls has been inferred from the presence of hyoid apparatus (Warren and Hutchinson, 1983; Rinehart and Lucas, 2013). As stereospondyl teeth show no shearing capacity it is most likely that stereospondyls swallowed prey with the use of a tongue and the retractor bulbi muscle, a method common in extant amphibians (Rinehart and Lucas, 2013) or with the use of inertial feeding as in extant crocodiliforme (Grigg and Kirshner, 2015). Rinehart and Lucas (2013) argued that inertial feeding was unlikely in stereospondyls as a rapid forward thrust of the head requires a neck, a structure which is absent in buccal pumping species (Clack, 2012). Inertial feeding can be used without a rapid forward movement (also referred to as ram feeding), gravity can assist with moving prey to the back of the mouth by tilting the head upwards and repeatedly opening and closing the mouth until the prey is at the back of the mouth where it can be swallowed, a mechanism used by crocodile and alligator species (Grigg and Kirshner, 2015). Using gravity in inertial feeding is more effective in air than underwater because of the buoyancy effect of water. It is more likely that surface dwelling stereospondyls rather than benthic species used inertial feeding to swallow their prey.

Body plans

Stereospondyl body plans are most similar to urodeles and crocodilians, though stereospondyl limbs are often not as heavily ossified. Most modern urodele amphibians swim with a laterally undulating movement of their tail and lower trunk (Lighthill, 1969). The larval and juvenile stages of *Archegosaurus dechini*, (Archegosauridae) from the Permian are considered to have swum in an eel-like fashion because they had poorly developed distal uncinat processes of the ribs, which

would have otherwise stabilised the trunk (Witzmann and Schoch, 2006). These processes were present in the anterior half of the trunk in adults of *A. dechini*, resulting in a more salmonid mode of locomotion, where the posterior half of the body is still doing most of the work, but anterior stiffness means an increase in speed with the decrease in flexibility. Stiffness is used by extant species that travel long distances, such as salmon and sharks. Witzmann and Schoch (2006) highlight the similarities between *A. dechini* and extant saltwater crocodiles from Australia, known to travel long distances in open water. *A. dechini* fossils have been described from deeper parts of freshwater lakes (Boy, 1977; Witzmann and Schoch, 2006). The narrowed snout of archegosauroids is consistent with fully aquatic hunters such as gharial crocodiles. What remains unknown is whether they actively pursued prey or if they ambushed their prey like most crocodilian and urodele forms. Crocodilians are amphibious and urodeles include terrestrial, aquatic and amphibious forms (Vitt and Caldwell, 2014).

Terrestriality amongst stereospondyls is not typically inferred from body plan differentiation, but from the amount of ossification of the postcranial skeleton with higher levels ossification indicates a more terrestrial mode of life (Witzmann and Schoch, 2006; Jeannot et al., 2006). Even the earliest stem stereospondyls were thought to have been capable of some short land excursions (Schoch and Milner, 2000). The Early Triassic Rhytidosteoidea and small Brachyopoidea resemble extant newt species in their skulls and body plans and (the earlier species) were very likely capable of foraging on land. Several Brachyopoidea species have been found in terrestrial deposits and though they have not been the subject of microscopy studies of the long bones, the small Brachyopoidea species may have been capable of land excursions to feed.

6.4 Functional comparative anatomy

Broadly speaking, prey seeking behaviours can be categorised in to sit and wait (ambush) or active (also known as wide foraging) (Vitt and Caldwell, 2014). Both can occur in the same ecosystem, creating niche partitioning through prey variety (Herrel et al., 2002). Most extant amphibians and reptiles use biting and grasping to acquire prey with both direct biting and suction feeding (Vitt and Caldwell, 2014). Suction feeding is achieved by rapid depression of the hyobranchial apparatus while

simultaneously opening the mouth causing water and prey to be sucked in to the mouth (Deban et al., 2001). Aquatic amphibians use suction or ram feeding, in the latter the jaws are accelerated over the prey and the buccal cavity is expanded to absorb the prey in a forward head movement over the prey with minimal involvement of the hyobranchial apparatus, and is seen in some salamander species (Deban and Wake, 2000; Nishikawa and Schwenk, 2002). Ram feeding can be achieved through many different means such as rapid head swipes, neck extension and full body propulsion using the tail or legs. As stereospondyls lack a flexing neck they would have to rely on rapid body movements or head swipes created by whole body movement. All of these mechanisms have associated morphological adaptations that assist in both seek prey and acquiring prey. These are discussed with respect to orbit position and overall skull shape below.

Comparative Anatomy of Vision

Most modern amphibians have near spherical eyeballs, with similarly shaped lenses (Schoch et al., 2014). The lens is a very stiff structure that bends little and the animal changes focus through the action of the *protractor lentis* muscle that moves the lens toward and away from the retina. Extant amphibians lack foveas so they have no areas of high visual acuity, but they are highly sensitive to changes in light. Anuran vision only allows them to view detail when movement occurs. They can only see in two scenarios, the object has moved, or they have moved (Ewert, 2004). The ability to move the eyeballs is variable in extant amphibians, Anurans are only able to retract the eyeball with the *retractor bulbi* muscle, whereas urodeles have completely moveable eyeballs. Some extant species have very reduced eyes, and most of these belong to the urodeles. The urodeles that do not have reduced eyes have trichromatic colour vision that they use to seek prey (Stebens and Cohen, 1995). They also have an oval pupil that may change the focal range between far and near sighted, in and out of water (Stebens and Cohen, 1995). Vision is an important factor to consider in prey seeking behaviour. The size and position of the orbits can provide a wealth of information on the niche occupation of different species.

Vision is a function of light (Hall and Ross, 2006) and the functioning of the vertebrate eye is determined by its size, the eye size is adapted to the needs of the species (Werner

and Seifan, 2006). The larger the eyes, the more space there is within the eyeball for the specialised visual cells, so more space means more cells, better vision (Vielieux and Kirk, 2014). It is likely that the vertebrate eye evolved only once (Hall and Ross, 2006) as they all have the same basic internal components. The vision type of a particular species will alter depending on the composition of the eye. Whether this is better acuity (focus) or light reception is determined by foveas and photoreceptors (Burton, 2008). Larger orbits have been associated with high locomotor speeds and active hunting (Kirk, 2006), presumably because longer axial lengths result in high acuity (Burton, 2008). Larger orbits amongst nocturnal species have also been found in birds (Garamszegi et al., 2002; Hall and Ross, 2006) and geckos (Wener and Seifan, 2006). Many frogs and salamanders exclusively rely on visual stimuli for prey acquisition (Deban et al., 2001; Vitt and Caldwell, 2014) particularly those that are sit and wait ambush predators (Vitt and Caldwell, 2014). Tadpoles of the pipid genera *Hymenochirus* and *Psuedhymenochirus* are suction feeders that have large frontal eyes that they use to direct their prey capture (Deban et al., 2001). *Lepidobatrachus llanensis* also use suction feeding in addition to a sit and wait ambush strategy to take large prey, likely identified visually as they have large and well developed eyes (Deban et al., 2001). Most reptiles are visual predators (Nishikawa and Schwenk, 2002).

The orbit is not an eyeball, but it can be used as a proxy for eye position and, to some extent, size. Eye position can clearly influence the field of vision and subsequent behaviour of an individual. Some extant anurans have shown capability, anatomically and behaviourally, for binocular vision (Pettigrew, 1986). Orbit shape and position varies between species of stereospondyls, from the metoposaur *Koskinodon perfectus*, which had round orbits positioned towards the front of the skull, to the Capitosauroidae, most of which had orbits much further back and central on the skull table. MacIver et al. (2017) proposed that the varied orbit positions seen across the fish to tetrapod transition were advantageous in different water and air combinations. The orbits moving to the top of the skull would allow better vision in shallow waters and at the water surface, whereas lateral orbits were more advantageous on land or in active swimmers (MacIver et al., 2017). In comparing the anteriorly positioned orbits of the metoposaur Trematosauroidae (see chapters 4 and 5) with the frontally placed orbit of pipid tadpoles it can be seen that the metoposaurs may have been able to

visually seek their prey at the water surface in the same manner as the tadpoles. The bite action would differ as the tadpoles use suction feeding, but the lack of preorbital skull interfering with the field of vision shows that metoposaurs may have employed a direct biting approach (rather than a head swipe) as they could keep the prey in sight in front of them for as long as possible. If metoposaurs lived in shallow waters they may have been able to propel themselves through the by pushing off the substrate at the waters bottom and using ram feeding to ingest its prey.

Larger orbits are frequently associated with nocturnal activities and low light environments (Werner and Seifan, 2006). Humphries and Ruxton (2002) suggested that the large eyes of the *Ichthyosaurus* were for both light sensitivity and visual acuity, allowing them to hunt for small prey in dark environments. However an increase in orbit size in amphibians could be indicative of their position in the water or on land, MacIver et al. (2017) showed that a significant orbit increase preceded the water to land transition in early tetrapods to facilitate better vision in air and associated the change with a crocodilian feeding strategy of viewing prey at the water's surface and so seeing in air not water.

The suggestions about eye function and orbit position in stereospondyls have been exclusively speculative (Schoch et al., 2014), but the orbit position features in several phylogeny reconstructions (Yates and Warren, 2000; Bolt and Chatterjee, 2000; Schoch, 2000; Warren and Marisicano, 2000; Damiani, 2001; Steyer, 2002; Steyer, 2003; Damiani and Yates, 2003; Schoch et al., 2007). These phylogenies placed little emphasis on the orbit, as no author uses more than two characters to describe the size, shape and position of the orbits. The impact of this is only minimally discussed in phylogeny papers, if at all, though some attempts have been made to infer patterns of vision in stereospondyls in species descriptions. Dorsolaterally facing orbits were considered to be suggestive of a passive hunting strategy in the Trematosauroida *Watsonisuchus magnus*, either at the surface, or on the bottom of the water (Steyer, 2003, Figures 6.11 and 6.12) and central orbits were associated with surface dwelling prey seeking in *Cherninia denwai*. The latter species is not well preserved but it does resemble a general capitosaur.

Extant amphibians can be grossly characterised as having laterally spaced eyes, similar to those that were identified in Brachyopoidea, metoposaur Trematosauroida and Rhytidosteoidea. The height of the extant amphibian skull may make some species

appear as though their eyes are further up on the skull, but they are not on top of the skull as seen in crocodilian species and some fish species (Vitt and Caldwell 2014). The distance from the anterior margin of the skull varies amongst amphibians, but the lateral orientation does not and so when examining potential life histories of stereospondyls it is important to look beyond the amphibians for comparisons for Capitosauroidae and Rhinesuchidae.

The anterolateral orbit positions of Brachyopoidea, metoposaurs Trematosauroidae and Rhytidosteoidea (see Figure 6.12) are similar to both terrestrial frogs and aquatic salamanders. The Chinese giant salamander *Andrias davidianus* (Figure 6.13), and other species of giant salamanders feed on small vertebrates and invertebrates (Fortuny et al., 2016) in freshwater streams (Vitt and Caldwell, 2014). Giant salamanders do not rely on their vision to seek prey, evidenced by their significantly reduced eyes, similar to the Brachyopoidea. Their sister taxon Hynobiidae consists of terrestrial species with similar skull shapes though less well articulated lower jaws, unfortunately their biology remains poorly understood (Vitt and Caldwell, 2014). Both groups of salamanders have laterally placed eyes, but eyes are much larger in the terrestrial species, consistent with visual cues for prey seeking, similar to the Rhytidosteoidea.

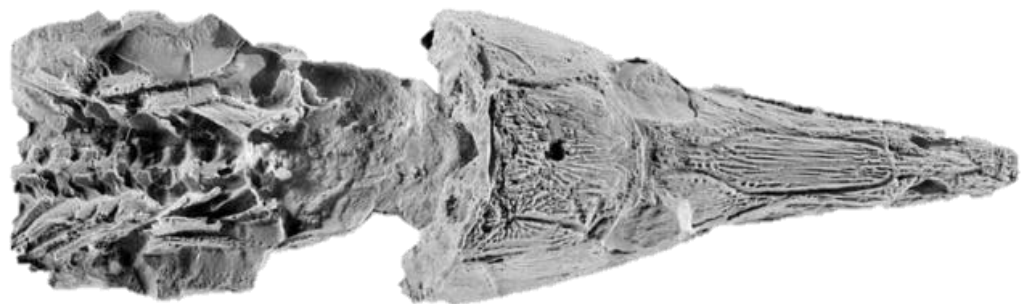
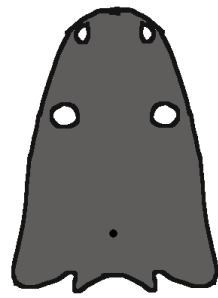
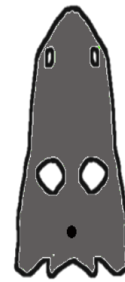


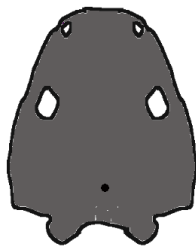
Figure 6.11 *Watsonisuchus magnus* with dorsolaterally placed orbits (Steyer, 2003).



Metoposauridae



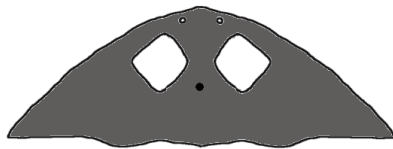
Archegosauridae



Brachyopoidea



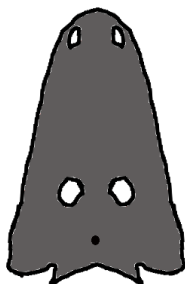
Rhinesuchidae



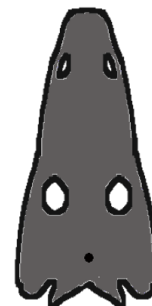
Plagiosauridae



Rhytidosteoidea



Capitosauroida



Trematosauroida

Figure 6.12 Skull shape and orbit position variation in stereospondyl families and taxonomic groups in dorsal view resulting from consensus shapes of principal component analysis (as seen in chapter five).



Figure 6.13 The aquatic *Andrias davidianus* (above source: London zoo) and terrestrial *Hynobius leechi* (below source per image copyright) showing lateral orbital placement common to extant amphibians.

Of stereospondyl groups with lateral orbits there is a distinct size difference between the Brachyopoidea and the Rhytidosteoidea, with the latter group having proportionally larger orbits. *Lydekkerina huxleyi*, a small member of the Rhytidosteoidea from the Lower Triassic of South Africa was considered terrestrial because of its tall skull and long bone microstructure (Canoville and Chinsamy, 2015). *L. huxleyi* exhibited a similar orbit positioning to several groups of terrestrial salamanders such as newts and European salamanders Pleurodelinae and Salamandrinae. It is important to note that this pertains only to overall skull shape and not the composition and presence of specific bones. *L. huxleyi* is morphologically representative of many other Rhytidosteoidea species with large laterally orientated orbits (Figure 6.14). Many of these species were small (skull length <10cm) with poorly developed sensory sulci (Schoch and Milner, 2000) and taller than typical

skulls, suggesting that terrestriality may have been more widespread than previously considered. Terrestrial feeding in salamanders is usually on slow moving prey such as invertebrates, using the tongue and jaws to acquire and swallow prey as seen in the Corsican fire salamander (Wells, 2007; Vitt and Caldwell, 2014).

Aquatic invertebrates are more widely reported from Triassic formations than terrestrial invertebrates. However, the terrestrial Glosselytrodea, Miomoptera and Protorthoptera have all been reported from the Triassic (Penny and Jepsen, 2014). In conjunction with lake-margin invertebrate assemblages and community level structures it shows that invertebrates were likely present in high enough numbers to sustain at least some predators (Roopnarine et al., 2007). Prey consisting of other amphibians and small amniotes is also possible.



Figure 6.14 The terrestrial Corsican fire salamander (*Salamandra corsica* source: wikicommons) showing lateral orbit placement and a short preorbital skull.

The aquatic salamanders use inertial feeding rather than the tongue acquisition of their land counterparts (Vitt and Caldwell, 2014). Slow moving prey are approached and ingested from a short distance, rather than a pursuit and catch, or sit and wait ambush strategies (Wells, 2007). Some stereospondyls may well have employed a similar strategy as their field of vision would have been comparable to many extant amphibians with laterally placed orbits. Laterally placed orbits are particularly useful for ambushing prey when there is little preorbital interference from the skull table, allowing an enhanced field of vision, as seen in chelydrid turtles (Vitt and Caldwell, Figure 6.15). The two post Triassic Brachyopoidea species were much larger than their Early Triassic counterparts, probably too large to be viable for terrestrial hunting. The

Jurassic *Siderops kehli* skull outline was very similar to the skull outline of the Japanese giant salamander, *Andrias japonicas* (Chapter 4 and electronic appendix EA2). *Andrias japonicas* is a fully aquatic species that lives in fast moving rivers, given the high levels of similarity between the late Brachyopoidea and the giant salamanders it seems highly likely that they shared prey ambushing behaviours. It is possible that *Siderops* was too large to create sufficient suction for the suction behaviour used by giant salamanders (Fortuny et al., 2015) but they could still be benthic ambush predators that used ram feeding.



Figure 6.15 Alligator snapping turtle *Macrochelys temminckii* (source wikicommons) waiting to ambush prey but maintaining a forward field of vision due to the lack of preorbital snout.

A final note on the anterolateral orbit position of extant amphibians; these species are frequently either fully terrestrial feeders or they seek prey at the surface whilst fully submerged in water. Amphibians are not reported as acquiring prey whilst waiting at the surface of the water, with the exception of larval foragers (Wells, 2007; Vitt and Caldwell, 2014). This observation is of particular interest when attempting to discern the habit preferences of stereospondyls.

In addition to the many species of stereospondyl that have lateral and anterolateral orbits, there are just as many that have orbits that are much closer to the mid line of the skull including the earliest stem stereospondyls (see Figure 6.16). Crocodilians are a much more suitable analogue for these stereospondyl species as many crocodilian species have orbit positions that are comparable and crocodilians are often used in stereospondyl literature (see figures 6.12 and 6.16). Conversely to amphibians which are frequently terrestrial or fully submerged aquatic feeders, crocodilians are very often surface dwelling ambush predators as discussed by MacIver et al. (2017) who proposed the same feeding modality for early tetrapods. Stem stereospondyls were

likely the same as the other early tetrapods. It is a common observation that animals which have eyes on the top of their head do not acquire prey on land. Restricting the visual field in this manner is not conducive to acquiring ground dwelling prey. This is true of crocodilians which have orbits on the top of their skull and use water to hunt a variety of prey. In addition to the stem stereospondyls, the central orbital placement is also in Rhinesuchidae and Capitosauroidae.

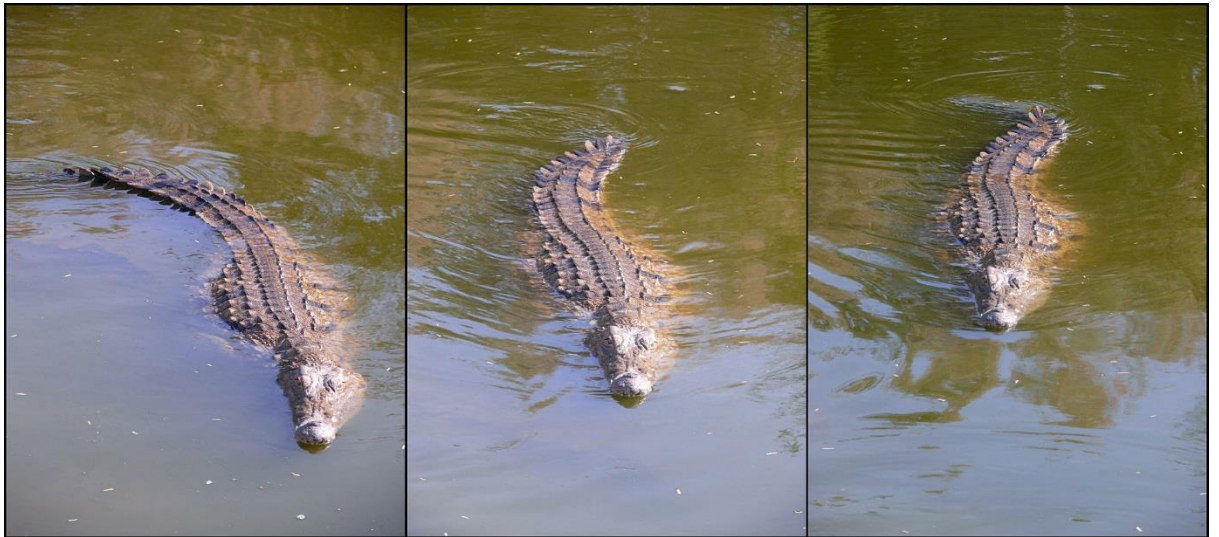


Figure 6.16 Nile crocodile *Crocodylus niloticus* (source wikicommons) actively seeking prey at the water surface

In summary, orbit position and eye size in extant amphibians and crocodilians are indicative of habitat and prey seeking strategy. Laterally orientated orbits are not associated with surface dwelling but either fully aquatic or terrestrial prey seeking, the differentiation cannot come from orbit position alone, but must incorporate other morphological details such as skull shape. Centrally placed orbits at the posterior of the skull table are associated with surface hunting as seen in many large crocodilian species.

Skull shape effect of feeding modalities

Differences in skull shape can reflect different resource use within a habitat as vertebrates are well known to show a correlation between cranial morphology and diet (Herrel et al., 2002; McBrayer, 2004). Feeding modalities are believed to be key to stereospondyl evolution (Fortuny et al., 2011) and stereospondyls are considered to have been top predators in their ecosystems in the Triassic, after the end Permian mass

extinction (Schoch, 2014). Different feeding modalities would suggest different prey types and subsequently different niches and ecotypes. The skulls of stereospondyls can give insights into their feeding morphology through their shape and anatomy. Skull shape is functionally very important to characteristics involved with locomotion and feeding (Fortuny et al., 2011).

The shape of the skull has been used as a phylogenetic character in many analyses (Yates, 1999; Bolt and Chatterjee, 2000; Yates and Warren, 2000; Schoch, 2000; Warren and Marisicano, 2000; Damiani, 2001; Steyer, 2002; Steyer, 2003; Schoch et al., 2007; Schoch 2008; Schoch and Witzmann, 2009; Dias da Silva and Marisicano, 2011; Fortuny et al., 2011). Despite the complexity of skulls the number of skull shape characters that feature in these matrix-based parsimony phylogenies varies from one (see Bolt and Chatterjee, 2000; Damiani, 2001; Dias da Silva and Marisicano, 2011, Fortuny et al., 2011) to a maximum of three (Schoch, 2000). The characters also feature seemingly subjective language such as “simple rounded or sharp edged” (Yates and Warren 2000), “slightly convex” (Dias da Silva and Marisicano, 2011), and “much elongated and narrow” (Schoch, 2000). Given the importance of skull shape to life history characteristics, and the range of skull shapes revealed in chapter 4, it certainly warrants a closer examination.

Skull shape across extant amphibians and reptiles can indicate their most likely prey seeking behaviour (in conjunction with other factors), active foragers typically have heads that are longer than they are wide whereas ambush predators are more included to be short and wide (Vitt and Caldwell, 2014). A narrow snout facilitates piscivorous crocodilians in their prey acquisition tactic of a rapid head swipe (Nishikawa and Schwenk, 2002). Wider heads are positively correlated with increased prey size in lizards (Vitt and Caldwell, 2014) and increased bite force in skinks (Vanhooydonck et al., 2011). Larger heads and robust jaws are seen in the salamanders Ambystomatidae and Dicamptodontidae which have been reported to eat small mammals (Deban et al., 2001). Head shape can also indicate habitat preference and aquatic salamanders are usually distinguishable from their terrestrial feeding counterparts by their reduced eyes and flatter heads (Wells, 2007). This flattened head is common among aquatic anurans and urodeles (Vitt and Caldwell, 2014) and has water resistance advantages facilitating easier prey acquisition, particularly amongst larger species (Schoch, 1999). We

demonstrated in chapter 4 that even just in dorsal view the skulls of the burrowing caecilians were significantly longer and narrower than urodele and anurans.

Stereospondyl skull shape has frequently been used to infer their diet but with limited comparative anatomy beyond descriptions such as “garial” (Steyer, 2002), or crocodiliform (Fortuny et al., 2011) or simply “short faced” with no reference to extant species (Maganuco et al., 2014). Works such as that of Steyer (2002) and Maganuco et al. (2014) described the biting action, in relation to head shape, but these were limited to a single species. Fortuny et al. (2011) assessed skull strengths across five species with Finite Element Analysis, none of which were species with short snouts.

Steyer (2002) postulated a piscivorous lifestyle for *Wantzonosaurus elongatus*, because of its long and narrow snout. Less resistance is generated in water by a narrow snout allowing it to move faster (Maganuco and Pasini, 2009), so this characteristic is often associated with piscivory (Witzmann and Scholz, 2007). The preorbital narrowing snout is a shape seen in some Alligatoridae, Crocodylidae and of course Gavialidae. Fish are also the main prey of the equally narrow snouted false garial *Tomistoma schlegelii* (Muller, 1838). Most narrow snouted crocodilians have laterally orientated orbits which is also seen in the lonchorhynchine trematosaurs and archegosauroids with similarly shaped snouts (Figure 6.12). The narrow snouted crocodilians catch fish with rapid lateral head swipes, an action that can be hastened with a short neck (Rhinehart et al., 2015). Additionally lateral head swipes can be created with a whole body movement, made more efficient in aquatic with a narrowed snout as seen in some dolphin species (Witzmann, 2006). In extant gharials, though their bite force is similar to wider snouted crocodiles, their loading force is lower, so they are restricted to more pliant prey (Erikson et al., 2012). Loading force is the force required to oppose the force of another object (created by mass multiplied by acceleration) so the gharial jaw cannot bite very hard prey such as turtles. A narrow snout, as seen in some stereospondyls (e.g. *W. elongatus*) probably would not have had the strength to crush large prey items, or hold strong and struggling prey for long (Witzmann and Scholz, 2007).

Unfortunately there are no extant amphibious analogues for this narrow snouted stereospondyl shape. Certainly there are species that are described as narrow snouted in their common name, but the snouts do not achieve the shape seen amongst the trematosaurs and archegosauroids (Figure 6.12). Amongst the aquatic amphiurans,

salamander species from North America, elongated rostrums and have been described as active hunters with an opportunistic diet (Vitt and Caldwell 2014, Figure 6.17) and an anecdotally strong bite suggested from the presence of hard shelled invertebrates as well as snakes in their diet. An additional stereospondyl similarity is the second row of teeth on the palate.



Figure 6.17 *Amphiuma means* (source as per image copyright) an aquatic urodele that is described as having an elongated rostrum (Vitt and Caldwell, 2014).

The anuran *Nasikabatrachus sahyadrensis* has a pointed snout and feeds on termites in burrows. The pointed snout is the only similarity with stereospondyls, *Nasikabatrachus sahyadrensis* has a distinctly rounded body and uses tongue protrusion down a buccal groove to acquire prey (Figure 6.18). Burrowing and tongue protrusion have never been suggested as a mode of prey acquisition amongst stereospondyls and the first evidence of prehensile tongues came later in the fossil record than stereospondyls (Iwasaki, 2002).



Figure 6.18 *Nasikabatrachus sahyadrensis* (source wikicommons) one of few anurans which a pointed rostrum, but the species lacks any other similarities to stereospondyls.

The tongue-less toad *Pipa pipa* has a distinctively triangular head but a much shorter rostrum than the lonchorhynchine trematosaur and archegosaur. The toad is a fully aquatic predator that acquires prey at short distances by grasping it with forelimb or engulfing it with suction feeding. The flat and arrow-shaped skull will reduce water resistance whilst the shortened snout would increase the ease of using the forelimb to put food in the mouth. The foreshortened faces are similar to the Rhytidosteoidea (see *Mahavisaurus dentatus*, Figure 6.19). There is no evidence that any stereospondyls had a manus that would use the prey grabbing technique that *Pipa pipa* use, however the *Pipa pipa* are known to wait in ambush in aquatic environments (Figure 6.20). The flattened and triangular skull would reduce drag underwater so it is possible that the similar Rhytidosteoidea if they were aquatic were also under water ambush predators. Lunging towards prey would displace it in water (Wells, 2007), a flat and triangular head in conjunction with suction feeding would reduce water resistance. Plagiosauridae stereospondyls have even been suggested to have the capabilities for suction feeding due to the structure of their hyoid apparatus (Schoch et al., 2014). Although Plagiosauridae orbits are much larger than the Rhinesuchidae, their skulls are also short and triangular with little preorbital area (Damiani et al., 2009).

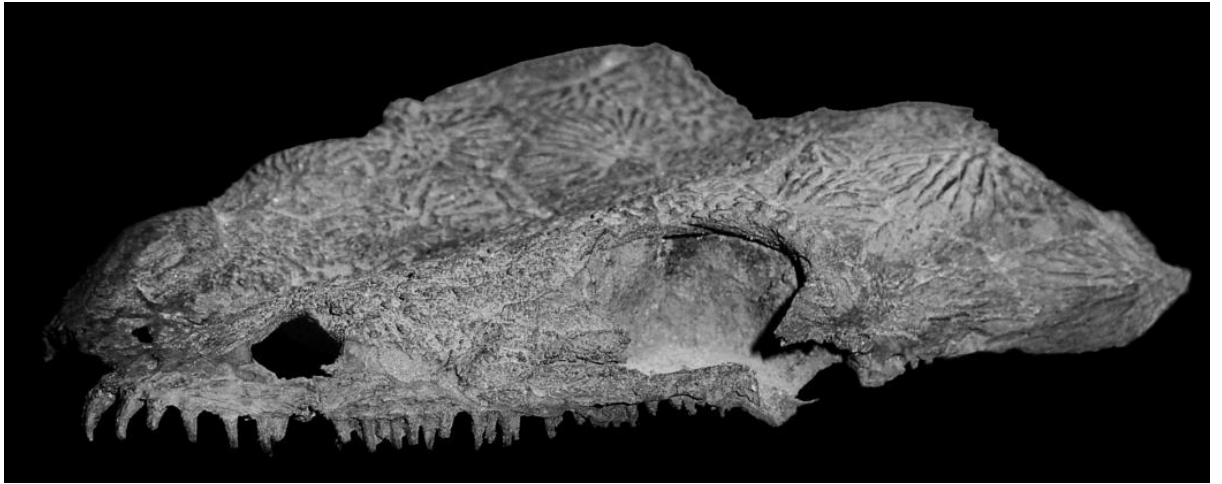


Figure 6.19 The short faced *Mahavisaurus dentatus* MNSM V6238 in anterolateral view from Maganuco et al. 2014



Figure 6.20 The *Pipa pipa* toad of South America (source as per image copyright) showing a short face similar to the Rhytidosteoidea and Plagiosauridae

Maganuco et al. (2014) briefly discussed the possibility of a semi-durophagous diet in the short faced *Mahavisaurus dentatus* based on the short and wide palate bones. The hard-shelled prey envisioned by the authors was the mid-water column nautilus-type species. Durophagy has been reported in amphibians such as the crab-eating frog *Fejervarya cancrivora* of Asia, which consumes insects and small crabs. It is described as having a narrow and rounded snout with few teeth on the vomerine ridge. Despite its common name it is a more generalist insect eater and little information is available on the anatomical adaptations to its diet. Two African *Tornierella* (*Paracassina*) species have enlarged gapes and structurally reinforced skulls which bore recurved teeth to eat snails. Heavy ossification of the palate is seen in several stereospondyl species including *Mahavisaurus dentatus* (Rhytidosteoidea) *Koskindodon perfectus* (Metoposauridae) and *Gerrothorax pulcherrimus* (Plagiosauroidae). All have wide palatine and ectopterygoid elements.

Most anurans are generalist predators whose prey can be predicted from general proportions (Wells, 2007). Wide heads and long jaws are associated with large and slow moving prey, narrow heads and short jaws are associated with smaller prey (Wells, 2007). Gape size is a function of skull, occipital and jaw mechanics and is often reported as “large” in stereospondyls and more so in wide-headed species (Schoch, 2006; Witzmann, 2006; Jenkins et al., 2008). Dentition (tooth row length) has been used as an indication of gape amongst temnospondyls (Carroll and Holmes, 1980; Schoch, 1998) and tooth row was remarkably conserved across all groups (Penrice and Deeming, 2016). For this reason we might cautiously consider tooth row length of the upper jaw a non-restricting factor in prey seeking behaviour and choose instead to focus on skull shape. Gape size has a twofold importance, firstly it is indicative of the size of prey that can be captured, but secondly it has inferences of potential bite force as higher bite forces are generated at the posterior of the mouth in lizards (Curtis et al., 2010). The bite force predictions come from an analysis of *Sphenodon* reptiles which have much taller skulls than stereospondyls, but similar findings were reported by Sellers et al. (2017) for flat headed crocodilian species *Alligator mississippiensis* and by Nogueira et al. (2009) in bats.

Hard shelled prey need a greater bite force which can be achieved in several ways (Schlaerken et al., 2012). Some of these are not possible to detect in extinct species without soft tissue (such as adductor muscle architecture) but reducing the jaw out

lever (jaw length) in relation to the pivot point can illustrate increased bite strength. Skull and mandible depth variation can influence the metric but if these are constant then a short lever (jaw) will produce a greater bite force at the anterior point than a longer one. Additionally, lamellae sutural connections that spread stresses and reduce torsion (Kathe, 1999; Fortuny et al., 2011) are found at greater proportions in wider headed stereospondyls (Kathe 1999) indicating that there is a greater need to disperse stresses in these skull shapes.

The large size of the Capitosauroides led Ochev (1966) to believe they were benthic ambush predators, with skulls reaching lengths of up to 1.5 metres (Penrice and Deeming, 2018, chapter 5, Schoch and Milner, 2000). The Capitosauroides were also characterised by a long and wide preorbital area creating a large snout (Figure 6.12). Their skulls shape is more similar to *Alligator mississippiensis*, *Caimen palustris*, and *Crocodylus niloticus* (Figures 6.9, 6.10 and 6.19). *Alligator mississippiensis* exhibit positive allometric growth through ontogeny and an 800 fold range in bite forces which likely reflect their dietary shifts through growth (Erikson, 2003). The snouts become wider throughout their life as head depth remains constant, resulting in greater stress resistance.

The width of the skull at points along its length can increase or decrease water resistance in forward movement, more surface area facing the direction of travel means more resistance (Fortuny et al., 2011). Narrow snouts are frequently associated with aquatic hunting as they are able to move through water with less resistance (Witzmann, 2006), but wider skulls will have more resistance in water. A common occurrence in crocodylians is to remain at the water surface (Erikson et al., 2012; Vitt and Caldwell 2014), meaning that a skull lift would move the upper jaws through air and not water, so resistance would be lower, reducing the effort required to lift the skull.

6.4 Conclusions

This comparison between stereospondyls and extant species has demonstrated that the skull shape, when used in conjunction with orbit position can provide strong evidence for both the prey type and where they were likely to seek that prey. Narrow snouts are capable of moving quickly in water but cannot withstand high levels of stress, so piscivory is the most likely mode of feeding particularly when paired with

laterally orientated orbits which would have an increased field of vision. Large and wide snouts would be difficult to lift through water but could take large prey which combined with orbits in the centre of the skull table would indicate a surface dwelling ambush mode of living as seen in modern crocodiles and alligators. Finally, semi-durophagous diets would be possible both in a fully aquatic or terrestrial environment for species with short and wide skulls with lateral orbits who could ambush or forage slow moving prey. The terrestrial or aquatic element can be inferred through skull height and size. In conclusion, this review of extant amphibians and select reptiles has provided a basis for creating a fuller picture of stereospondyl life histories. This picture shows there is scope for many more life history characteristics than previously envisioned for stereospondyls, as well as further evidence for previously suggested piscivorous and terrestrial life styles. This information must now be brought together with the geometric morphometric data and the fossil record analyses to create a narrative of stereospondyl evolution.

Chapter 7: Functional morphology of stereospondyl amphibian skulls

7.1 Overview

There were significant changes in the functional morphology of stereospondyls as they progressed through evolutionary time. The evidence presented throughout this thesis shows that the stereospondyl groups, which are all present at different points in the fossil record, differ in their skull shapes and this reflects their prey seeking behaviours and so life history characteristics. The present chapter will discuss each taxonomic groups of stereospondyls in the context of their time and location and how they were adapted to the environment in which they lived.

As shown in chapter 3 (in particular see Figure 3.13) the stem stereospondyls appeared in Europe in the Carboniferous and remained until the end of the Permian. The Archegosauridae also appeared at the end of the Carboniferous and lasted for the duration of the Permian. The Rhinesuchidae, Rhytidosteoidea and Brachyopoidea appear in the fossil record in the Late Permian, and these taxonomic groups survived the end Permian mass extinction. In the Early Triassic these taxonomic groups were joined by the Capitosauroida and lonchoryforme Trematosauroida. Finally, the Plagiosauroida appeared and disappeared in the Middle Triassic, along with the Metoposauridae, which persisted until the Late Triassic. The Metoposauridae had been thought by some to be a part of the Trematosauroida (see Schoch and Milner, 2000), but their distinct morphology supports the second school of thought which places the Metoposauroidae outside of the Trematosauroida (see Maganuco et al., 2014).

The stereospondyls had a global distribution and have high recorded numbers from Europe and Africa. Their fossil record, as with all fossil records, is biased by the availability of the fossils in the rock. In particular the stereospondyl record has large gaps from the Middle Triassic and the Jurassic (Chapter 3). The greatest sources of skull variation lay in the overall outline with shapes ranging from more than twice as long as they are wide, where rostral narrowing begins immediately in front of the orbits, to those that are as short as they are wide, the position of the orbits on the skull table was an additional source of variation (Chapter 4), with each group showing a

characteristic shape (Chapter 5). These changes are interpreted to reflect differences in prey seeking behaviour and so life history characteristics (Chapter 6). The diversity within stereospondyl groups varied but was not explicitly associated with high species numbers. The information gathered in this thesis will be synthesised in the following pages to illustrate why stereospondyls were the most successful clade of early tetrapods and why they ultimately went extinct.

Sections 7.2 to 7.6 discuss the evolution of stereospondyl skulls through time and how the skull shape changes altered how the different taxonomic groups could interact with their environment.

7.2 Carboniferous and Early Permian

A northern origin of stereospondyls was advocated by Schoch and Milner (2000) and my wider consideration of the Stereospondyl, supports this perspective (see chapter 3). The stem stereospondyls were present alongside the Archegosauridae in the Northern parts of the supercontinent Pangea in the Carboniferous and Early Permian (Benton and Newell, 2014) in what is now Europe. The stereospondyl's closest ancestral clade are believed to be the Eryopidae (Schoch, 2014). Eryopidae were small to large terrestrial amphibians present in North America and Europe in the Carboniferous and Permian. Stereospondyls were not found in North America until much later.

The earliest stereospondyl, *Capetus palustris* was present before the rainforest collapse induced by the ice age at the end of the Carboniferous (Sahney et al., 2010). The Archegosauridae also arose before the end of the Carboniferous, both the stem and the Archegosauridae were able to continue into the Early Permian whilst non stereospondyl amphibians declined (Benton et al., 2013, chapter 3). The comparison of extant species in Chapter 6 showed us that the stem stereospondyls appear to have most likely been capable of walking on land but were most likely to have sought prey in an aquatic environment. Stem stereospondyls would not have been actively seeking fast moving prey because widened skulls and centrally placed orbits make stem stereospondyls unsuited for fast swimming and their orbit placement would reduce lateral visibility. The aquatic nature of the stem stereospondyls would have had a two part advantage, they would not have been in direct competition with the much larger

Eryopidae (Pawley and Warren, 2006) and they would be somewhat buffered against the volatile Permian climate (Clapham and Payne 2011; Gardner et al., 2011).

Pangea's interior was arid (Roscher et al., 2011), which was an unfavourable climate for water seeking amphibians (Frobisch et al., 2010). The Early Permian bore the scars from the Carboniferous ice age as it had few forests (Benton and Newell, 2014), but a wet climate in the north of Pangea provided an ideal location for an uncontested amphibian diversification (Benton et al., 2013; Chapter 3). The continuing arid environment of central Pangea would have likely imposed restrictions on dispersion of early stereospondyls although it may have had less effect on the more terrestrial amniotes around at the time (Fortuny et al., 2015).

The Archegosauridae had more species with narrow heads than the stem stereospondyls. The eyes were central or anteriorly placed in the skull and they were relatively closer together in smaller species. This eye position is not ideal for a forward bite because they may lose sight of the prey before securing it (Fortuny et al., 2011), but they were well positioned for a rapid swiping motion of the head prior to biting (Fortuny et al., 2011). However, the narrow snouts are likely to have been associated with low bite strength (Anderson et al., 2013; Penrice and Ruta, 2017). The narrow snout may have been further weakened by the arrangement of palatal bones because the maxilla is further back in the palate, creating a suture between the maxilla and premaxilla at the middle of the tooth bearing region, potentially decreasing bite strength. The full bite potential of the Archegosauridae would require more analysis to include the skull height but it is clear that they were competitively advantageous over the stem stereospondyls in fast aquatic movements and were not in competition with the more numerous terrestrial species.

Anteriorly narrowed triangular heads are well adapted to swimming because they have less resistance in water (Fortuny et al., 2011; Schoch, 2014; see Chapter 6). This would suggest that Archegosauridae were active swimmers most likely seeking fish, which they could acquire and kill quickly. As mentioned in Chapter 6, piscivory is common amongst narrow snouted crocodylians and dolphins without obviously triangular heads.

The aquatic nature of adult Archegosauridae is not a novel suggestion (Witzmann, 2006; Schoch and Witzmann, 2009; Fortuny et al., 2011), but this is the first time it

has been studied in the context of a wide range of species in all taxonomic groups. Other studies have only compared one or two species (Witzmann, 2006; Schoch and Witzmann, 2009; Fortuny et al., 2011), while the present study has used all available complete skulls of Archegosauridae species (eight skulls total, see electronic appendices 1 and 2) to give a much greater coverage of the clade. The present study is also the first time that more than the shape and dermal sculpturing of the skull has been used as evidence for aquatic living. The palate, orbit and nares positions all support an active swimming and hunting way of life (see Chapters 4 and 6). The Archegosauridae had uncinat processes on their ribs, which act to stabilise the thorax in a salmonid mode of swimming, seen in long in distance swimmers such as sharks and salmon (Witzmann and Schoch, 2006) strengthening the argument for an aquatic lifestyle. Uncinate processes are also present in most extant bird species where they often serve as a site of attachment for the scapula muscles, which also helps to stabilise the trunk and aid in respiration (Tickle et al., 2007). The role of the uncinat process in respiration is such that longer processes, as seen in Archegosauridae, help to make respiration more efficient. The uncinat processes were also present in *Ichthyostega*, another aquatic early tetrapod (Kardong, 1995). The processes likely aided in both respiration and trunk stabilisation, allowing Archegosauridae to swim effectively, using less energy, but also being able to inhale large volumes of air, as the scaled stereospondyls did not use their skin for additional oxygen consumption (Witzmann, 2015).

Both the stem stereospondyls and the Archegosauridae persisted in the fossil record until the mass extinction at the end of the Permian. The European overlap and multistage persistence in the fossil record would mean that some kind of niche differentiation would be needed in order to prevent competition between species of stereospondyls. Their northern distribution correlated with the presence of glaciers in the south (Benton and Newell, 2014), and the skull shapes of the stem stereospondyls and the Archegosauridae show that they were likely adapted to different modes of living.

7.3 Late Permian

As well as the stem stereospondyls and Archegosauridae three new taxonomic groups appeared in the Late Permian, the Rhinesuchidae, Brachyopoidea and Rhytidosteoidea. By this point in the Late Permian, the stem stereospondyls stayed in the north whereas Archegosauridae were more globally distributed (see Chapter 3). Despite the new additions, the Late Permian was a relatively slow period in stereospondyl species turnover. Examination of the fossil record shows that once stereospondyls had established a global distribution, their rates of origination and extinction were low until the end of the Permian (see Chapter 3). The terrestrial and aquatic environments were not erratic or rapidly changing in the time leading up to the end Permian mass extinction, unlike what was happening in the marine environment due to changing CO₂ levels (Benton and Newell, 2014). This stability may have been reflected in the stability in turnover of stereospondyls.

Species in the Rhinesuchidae and Rhytidosteoidea, which first appeared in the Late Permian, had similar skull outlines to the stem Stereospondyls but the skulls of the latter were much smaller in length than the former (see Chapter 5). Additionally the orbital placement disparity highlights the differences in prey seeking behaviour (see Chapter 5, Figure 5.3). The Rhinesuchidae were more likely to be filling a similar role as the stem stereospondyls and taking advantage of an otherwise unoccupied aquatic ambush niche, as their orbits were dorsomedially placed. The larger size of the Rhinesuchidae may have made them less suitable for extensive land travel since large and heavy skulls are easier to support in water. A microscopic inspection of the postcranial skeleton would be necessary to confirm this as the medullary composition of long bones is indicative of their life style (see Sanchez et al., 2010). The anterior nares position would allow the animal to lift only the nares out of the water to breathe which implies that they did not need to reside at the surface and so may have had commonalities with the lifestyle of the Chinese Giant Salamander (Ultsch, 2012). The Rhinesuchidae did not overlap with stem stereospondyls nor the Eryopidae (the family is not known after the Early Permian according to Benton et al. (2013) so were probably the only stereospondyls of their size in their environment.

The smaller Rhytidosteoidea would not have been in competition with Rhinesuchidae even though they have both been found in modern-day India and South America. Rhytidosteoidea prey would have been small and quite possibly terrestrial (Chapter

6). The Brachyopoidea, which also first appeared in this Epoch, had much wider skulls with further anterior orbits. The later Brachyopoidea were larger and had flatter skulls than the Rhytidosteoidea but several of the earlier species were small (see chapters 5 and 6). Many species of Brachyopoidea have been collected from terrestrial deposits but the species frequently had well developed lateral line sulci suggesting at least some aquatic foraging or living (such as breeding) (Damiani and Warren, 1996). Brachyopoidea also ranged in size from small (skull lengths of 9cm) to large (skull lengths of approximately 50cm) so would have had a range of prey sizes within their group. The Brachyopoidea were the longest lasting group of stereospondyls, and their ability to seek prey on land (as detailed in Chapter 6) and in the water may have made them adaptable to changing environments, or their diversity helped them reduce competition from species in the same environment (discussed further in section 7.7).

By the Late Permian the last effects of the Carboniferous ice age had disappeared and temperatures were milder (Benton and Newell, 2014), though there was still a vast central continental desert (Roscher et al., 2011). More amniotes than amphibian species were on land by the end of the Permian (Fortuny et al., 2014), even so, by the Late Permian, stereospondyls had reached the southern continent of Gondwana (Dias da Silva et al., 2006).

In general terms, environmental change can cause species to disperse away from their original habitat and so they alter their geographical distribution (Ronce, 2007). As shallow coastal and lake waters became warmer (Benton and Newell, 2014), they may have provided a route for the well adapted swimmers, the Archegosauridae, to reach Southern continents by connected water routes. A detailed palaeomap and knowledge of the directional flow of rivers, and the location of the drainage systems (such as that found in Miller et al., 2013) could form the basis of a geographical information system study to test this theory. Stem stereospondyls, as described here, never made it out of Europe, perhaps because they were poorly adapted for long distance swimming, but the Archegosauridae had now reached the area that is now South America too. India had four groups of stereospondyls.

The Rhinesuchidae, Brachyopoidea and Rhytidosteoidea persisted through the largest known mass extinction, but the species turnover was nearly 100%. Only the South American *Arachana nigra* may be considered as being from both the Permian and the Triassic, but this single specimen was found in a horizon that crosses the Permian

Triassic boundary (detailed in chapter 3, Pinero et al., 2012). Its attribution is due to a lack of precise dating on the formation, not because it has been found in deposits from both time periods. Environmental instability increases rates of extinction (Drake and Lodge, 2004; Adler and Drake, 2008) and the end Permian mass extinction, which lasted between 100,000 and 200,000 years (Roscher et al., 2011), saw substantial environmental change (Benton and Newell, 2014). This resulted in the completely different species composition of the stereospondyls (see Chapter 3).

7.4 Early Triassic

The Early Triassic was an interesting time in the history of stereospondyls. Stereospondyl and non-stereospondyl amphibians had a truly global distribution in the Early Triassic (Shishkin et al., 2006) although stereospondyls account for the majority of amphibian species present (Benton et al., 2013, Chapter 3). The Early Triassic saw the beginnings of two new, and highly speciose taxonomic groups, the Capitosauroidae and Trematosauroidae. Skulls of the former were structurally more similar to the wide headed Rhinesuchidae and Rhytidosteoidea whereas the early (lonchoryforme) Trematosauroidae species had head shapes that were more similar to those of the Archegosauridae.

Greenland, which was at the northernmost point of Pangea, was host to some very interesting garial-like types from the lonchoryforme Trematosauroidae, though what it was about Greenland that made it an ideal home for these species, is hard to say. Unfortunately, most of the literature on Greenland's Early Triassic climate is centred on its deep marine environment, so less is known about the freshwater stereospondyl habitats. These lonchoryforme Trematosauroidae appear to have used a similar niche to the Archegosauridae so we might consider that Greenland had some similarities in water bodies and prey availability as Late Permian Europe. We must wait for further palaeoclimatic research of Greenland's Early Triassic horizons to understand the reasons for the high occurrence of garial forms.

Like the Archegosauridae, the first lonchoryforme Trematosauroidae in the Early Triassic had relatively long prenasal snouts, e.g. *Wantzonosaurus elongatus*, *Aphaneramma rostrum* and *Tertrema acuta*, so they very likely to be actively hunting fish eaters. Whether this was a viable option given the orbit position would require a

more precise field of vision study in these taxa though their laterally positioned orbits are similar to other piscivores such as dolphins and garial crocodiles. Stevens (2006) did basic calculations of field of vision using the size and location of the orbits in relation to the snout in tyrannosaurs. Such a technique would probably apply to stereospondyls if the skull height was taken in to account, as in MacIver et al. (2017) although this would need to include the model of several different eye types, there is no clear way of knowing exactly the type of eyeball stereospondyls had (Schoch et al., 2014).

The lonchoryforme Trematosauroida, Capitosauroida and the Rhytidosteoidea were found concurrently in what is now Africa, in southern Pangea, and collectively they exhibit a lot of disparity. The lonchoryforme Trematosauroida occupied the role of active aquatic prey seeking, the Rhytidosteoidea would not have been directly competing with them as Rhytidosteoidea were likely to be seeking slow moving prey on land or in the water. The Capitosauroida would have sought much larger prey that it would ambush from the water surface. The analysis of the fossil record in chapter 3, which is in concurrence with Benton et al. (2013), showed that stereospondyls faced little competition from non-stereospondyl amphibians in the Early Triassic and other tetrapods were much slower to recover from the end Permian mass extinction so stereospondyls were largely competing only with themselves.

The area in Gondwana corresponding to modern day southern Africa was very dry (Pawley and Warren, 2005) but there were big and wide rivers with big estuaries (Benton and Newell, 2014). The properties of the rivers resulted from the absence of trees (inferred from a lack of coal deposits from this time; Benton and Newell, 2014), which meant that the water would have been very turbid because soil eroded by rain was washed into the rivers (Ward et al., 2000). Decreased habitat fragmentation resulting from the big rivers and estuaries would have meant smaller distances between habitats which could have provided a means of dispersal from the arid and competitive southern part of the continent to the wetter climes of Europe to the north (Benton and Newell, 2014).

Stereospondyl dispersion may have followed a stepping stone spreading pattern, where multiple movements occurred over an extended time period (Abrams, 1998, Carlquist, 1966). Disparity could increase with dispersal, creating a series of new species as stereospondyls returned to the north (Pease et al., 1989). However, the

morphological difference between two species would not have to be as great between new species if they were moving into new and unsaturated niches (Erwin, 2007). In contrast, those species that stayed in Africa seemed to have had to adopt new niches for themselves to avoid competition with other stereospondyls. This perhaps led to changes observed in the skull shape and the relative position of the orbits and nares as was seen in chapter 4.

The stereospondyl groups present in the Early Triassic did not seem to display the same amount of disparity within each of them. The analysis done in chapter 4 showed that the Capitosauroidae were remarkably conservative in their morphology, particularly interesting because they were very speciose. The same cannot be said for the smaller Rhytidosteoidea and lonchoryforme Trematosauroidae which were much more morphologically diverse as evidenced by the very large morphospace occupations in the geometric morphometric analyses.

The Early Triassic was a time of high dispersal and species turnover, but low establishment, as one third of all originations occurred in the Early Triassic but there was a high number of extinctions at the end of the Early Triassic (Fortuny et al., 2015). Lines of arrested growth in the long bones of Rhytidosteoidea show they lived short lives, maturing early (Cannonville and Chinsamy, 2015). This life history characteristic has been cited as a response to mass extinctions used by many early tetrapods (Botha-Brink et al., 2016). The species turnover was high, but the taxonomic groups fared well, only the already-rare Rhinesuchidae did not persist in to the Middle Triassic.

7.5 Middle Triassic

The Middle Triassic is a period of poor preservation for stereospondyls and their diversity in the fossil record was closely correlated with the number of fossil bearing rock formations. Extinctions in this time therefore may be an artefact of preservation bias. Analysis of the fossil record (chapter 3) showed that overall stereospondyl species numbers were low but non-amphibian tetrapods were on the rise and presenting a competitive and in some cases predatory threats to stereospondyls.

The final group of stereospondyls to appear, the Plagiosauroidae, appeared in the Middle Triassic. To date only three species have been found that are attributed to the

Plagiosauroidae (Damiani et al., 2009; Witzmann et al., 2012; Schoch et al., 2014). The Plagiosauroidae are characterised by extremely wide, short heads with enormous orbits and are considered to be the most unusual group within the stereospondyls (Damiani et al., 2009). Damiani et al. (2009) suggested that the head shape allowed them to employ suction-feeding whilst waiting on the bed of a body of water as a way of acquiring prey and Plagiosauroidae skulls were small enough to create sufficient suction. In effect, Plagiosauroidae stereospondyls may have simply caught their prey by rapidly opening their mouths as the prey swam by. Suction feeding is not likely amongst other stereospondyl groups as they either lacked the hyobranchial apparatus to achieve it or their akinetic skulls were too large to create sufficient suction. Though large extant animals employ suction (e.g. whales) their skulls have substantial kinesis and lack the extensive interdigitating sutures of stereospondyls (see Boutel, 2005). Aquatic salamanders catch their prey with suction feeding by quickly increasing their oropharyngeal volume which creates a suction to pull prey in to the mouth, facilitated by the hyobranchial apparatus (Fortuny et al., 2015). Cryptobranchid salamanders are fully aquatic extant species that have a wide and short head, similar to the Plagiosauroidae, to increase their gape for suction feeding (Traub, 1993) though the Brachyopoidae are much more similar in skull shape to the cryptobranchids. The Plagiosauroidae were so unusual they really lack any extant analogues. Even if both groups sought prey in an identical manner to cryptobranchids, the Plagiosauroidae would not have been in direct competition with the Brachyopoidae as they did not occur in the same time and place.

If orbit size is indicative of maximum eye size (Hall and Ross, 2006; Werner and Seifan, 2006; Schoch et al., 2014, MacIver et al., 2017) then the large orbits would suggest a dark, or very turbid, hunting environment for Plagiosauroidae as the analyses in chapters 4 and 5 showed that their orbits occupied much of their skull table. Whilst the orbits are the weakest point in any skull, an FEA study carried out on Capitosauroidae has shown that orbit size and location does not alter the overall stress patterns of the skull in stereospondyls (Marcé-Nogué et al., 2015). If this holds true for Plagiosauroidae, then their skulls may have been capable of withstanding substantial stresses in feeding.

The Metoposauridae first appeared in the Middle Triassic. Phylogeny studies support a European origin for the metoposaurs (Sulej et al., 2007; Brusatte et al., 2015). The

skulls were wider and the round orbits were much further anterior on the skull table than the lonchoryforme Trematosauroida. Metoposauridae were present across the Northern continents, as well as India. The origin and phylogenetic relationships of this unusual group has been the focus of most recent studies (Damiani and Yates, 2003; Sulej et al., 2007; Brusatte et al., 2015) but which have ignored the palaeobiology and functional morphology. The main investigation has been focussed on whether the Metoposauridae belong to the Trematosauroida. The skulls of the Metoposauridae were larger than the lonchoryforme Trematosauroida (Schoch and Milner, 2000) and were more similar to the Capitosauroida in that respect. The differences in orbit position between the metoposaurs (lateral, anterior) and capitosauroids (medial, posterior), identified in chapters 4 and 5, suggests very different prey seeking behaviours (discussed in detail in chapter 6).

The morphological diversification of the stereospondyls in the Middle Triassic was substantial and could have served to reduce competition between species. Niche availability can regulate species richness through competition for resources (Benson et al., 2016) and expansionism is possible when competitive interactions between species are rare (Svenning et al., 2014). There are two ways this is possible, a lot of niches created by the environment (e.g. the Early Triassic), or a lot of niches created by phenotypic variation (e.g. the Middle Triassic).

The Capitosauroida were the giant stereospondyls of Europe and Africa in the Middle Triassic and once established, they persisted in the fossil record for much longer than their Early Triassic ancestors. *Mastodonsaurus* and *Cyclotosaurus*, the two biggest genera, originated in the Ansinian and went extinct in the Norian and so lasted a period of 20.2 MYr (Benton et al., 2013). Larger species are better suited to cooler climates (Kingsolver and Huey, 2008; Gardner et al., 2011), and an increasing size of species in response to global cooling has been documented elsewhere in the fossil record and is referred to as Bergmann's rule when it is observed in extant species (see Sheridan and Bickford, 2011; Mora, 2013). Additionally, increased oxygen levels during the Triassic have been suggested as a facilitating factor for gigantism (Harris et al., 2006) but it was more likely to impact terrestrial species. Through this size change the Capitosauroida showed remarkably conservative morphology as indicated by the frequently small occupation of morphospace in the analyses reported in Chapter 4. Terrestrial tetrapods were recovering in the Middle Triassic and reaching large sizes

(Harris et al. 2006). Smaller surface dwelling and terrestrial stereospondyls may have been at risk from larger carnivorous theropods or been in competition with smaller carnivores. The large size of stereospondyls in the Middle Triassic may have been in response to the evolutionary pressure of large land carnivores. Fewer species of stereospondyl were originating in the Middle Triassic, and those that did were more disparate than their Early Triassic predecessors.

The multi-modal niche occupation is not a novel suggestion for stereospondyls' success. Maganuco et al. (2014) agreed with Steyer (2001), that phenotypic plasticity meant that stereospondyls could use a range of palaeoenvironments. This lack of competition between stereospondyls resulting from their morphological and so functional disparity could be why so many of the Middle Triassic species persisted in to the Late Triassic.

7.6 Late Triassic

There were no new taxonomic groups in the Late Triassic, the Rhytidosteoidea, Capitosauroida and Trematosauroida were all that remained. Though the Brachyopoidea have not been found in the Late Triassic fossil record, it can be assumed they were still present as Brachyopoidea remains have been found in younger deposits,. The Late Triassic saw more rain and monsoons globally (Preto et al., 2010) and whilst there were still giant stereospondyls in Europe the lonchoryforme Trematosauroida species with gharial-like skull shapes were now extinct. Generally, there was variation in the positioning of the orbits and nares, but less variation in general skull shape amongst these species, so there were still a lot of specialist niche occupiers.

Unfortunately for the stereospondyls, species can become trapped by their adaptations when their environments change. If a species cannot follow its niche, that is to physically relocate itself to remain in the same environmental conditions, because of a fragmented environment, then it is going to have to adapt. If it cannot adapt because it is very specialised then it is greatly at risk of extinction (Pease et al., 1989; Frobisch et al., 2010). Large species (see Chapter 5 for details on skull sizes) are also very vulnerable to extinction because they have slow life histories maturing late and breeding slowly (Cardillo et al., 2008). By the Late Triassic the stereospondyls were morphologically diverse in their functional morphology likely reducing competition

among themselves and with the large non-amphibian tetrapods. However in doing so they likely made themselves vulnerable to extinction.

The Late Triassic mass extinction was actually a series of smaller extinctions over a long time period (Lucas and Tanner, 2015). At the end of the Epoch there were warm and cool temperature fluctuations because of the Central Atlantic Magmatic Province (Lucas and Tanner, 2015) and the humidity changes in Europe caused local extinctions (Lucas and Tanner, 2015). The stereospondyl species extinction rate was too high and the originations were too low for them to recover. The skull shapes that had been so successful in the Middle Triassic were now shapes that tied species to their niches because of their specialised functional adaptations, but those niches were disappearing due to global climate change at the end of the Triassic, resulting from widespread volcanic eruptions. The stereospondyls were almost completely extinct at the end of the Triassic.

7.7 The stereospondyl extinction

After the Triassic, Australia became a haven for stereospondyls, the only two post-Triassic stereospondyl finds were species of Brachyopoidea (reported in the fossil record analysis of chapter 3). Brachyopoidea appeared after substantial gaps in the fossil record, but the later arid nature of Australia's climate is not conducive to fossil preservation. We must wait for more fossil finds to solve the puzzle of the Australian amphibians.

The end of the Triassic was the end of most of the stereospondyls. The advent of archosaurs with a crocodiliform morphotype (Benton et al., 2013), coincides with the demise of crocodiliform stereospondyls. The narrow snouted Trematosauroida declined as the equally garial reptilian phytosaurs (primitive archosaurs) were dominating the aquatic environments (Benton et al., 2013). Phytosauridae had a global distribution through the Late Triassic (Benton et al., 2013) that would have overlapped with the stereospondyls (chapter 3). The Phytosauridae were larger than the Trematosauroida (Stocker et al., 2013) and may have simply outcompeted the Trematosauroida by being larger or faster. On land, the Rhytidosteoidea were much smaller than the dinosaurian species that started appearing in the fossil record from the Middle Triassic (Benton et al., 2013). The body plan of the stereospondyls has never been modelled for gait and motion, but it clearly would not have had the mobility

of species like the theropod dinosaurs that are known from the Middle Triassic onwards (Benton et al., 2013).

The only stereospondyl group to survive was the Brachyopoidea which most resembled the modern day amphibians, particularly the giant salamanders. Gaps in the fossil record mean that we do not know why or when Brachyopoidea truly disappeared from India, but the climate in Australia and India was humid with large rivers and peatlands and the two modern day continents were adjacent in the Jurassic (Fawcett et al., 1994; Johnson, 2009). Archosaurs including aquatic phytosaurs and terrestrial Rauisuchidae have been found in India but not Australia (Benton et al., 2013). Archosaurs would have been very unlikely to be in direct competition with Brachyopoidea who likely ambushed aquatic prey at the water's edge or fully submerged as modern giant salamanders do. The large and wide Brachyopoidea skull would facilitate a generalist diet, much like the extant giant amphibians. The extant giant salamanders mostly inhabit fast flowing river systems which were not as common as swamps and peatlands in Jurassic and Cretaceous Australia (Fawcett et al., 1994; Johnson, 2009) but this would not interfere with ambush prey seeking. The shallow swamps could allow the large Jurassic Brachyopoidea to propel themselves toward prey using the bed of the body of water to create the propulsion for ram feeding. It is possible that Brachyopoidea were too large to be prey for narrow snouted phytosaurs. At present, there is no reptilian or mammalian fossil known with a similar skull shape to the Brachyopoidea, but there are many reptiles that resemble the other stereospondyls groups which were not found after the Triassic.

The amphibious stereospondyls were outlived by the reptiles with very similar skull shapes and body plans. Perhaps it was because reptiles were better adapted to land than amphibians (Harris et al., 2006). Stereospondyl scales amongst other adaptations, would have provided protection from desiccation to an extent, sufficient for small species to live on land and larger ones to make brief excursions, but their scales would not have been as robust as the thicker and more consistent scales of the reptiles, which were able to survive on land much longer. The reptile species' ability to survive on land would have meant that they were able to disperse across the large land masses of the Late Triassic and Early Jurassic in search of new environments as microclimates as global climates changed (Lucas and Tanner, 2015). The highly adapted

stereospondyls, which were tied to water for at least part of their life cycles (Frobisch et al., 2010) if not all of it, were unable to respond to the rapid loss of their ecosystems.

7.8 Future developments

One of the most obvious avenues of additional research is to use the rest of the stereospondyl skeleton in a study similar to the present one. The lower jaw and postcranial skeleton could provide a plethora of information to complement this new knowledge of the skull, walking or swimming speeds, bite strength would all add to the understanding of the evolution of these speciose early tetrapods. Postcranial and mandibular fossils are not as numerous as the skull finds, which is why they were not used here. In addition to the differences between the skeletons and mandibles of different species, it would be possible to look at the way that they change in relation to the skull. The current study has established a morphospace occupation for stereospondyl skulls, the other parts of the skeleton may or may not produce the same distribution in morphospace. The comprehensive character based phylogenies include elements of the entire skeleton. If a geometric morphometric study was carried out on the same areas then the resulting principal component scores could be used to create a phylogeny to compliment the traditional character based approaches. As the most comprehensive phylogenies include characters from more than just the skull and palate, the geometric morphometric study here would not be directly comparable with the published phylogenies. Validating the new phylogeny with existing ones would not be sufficiently robust to declare the new method appropriate without using comparable material.

Even without a full skeleton study geometric morphometrics can still assist character based phylogenies by objectively grouping shapes. Principal component scores cover a much broader range than discrete character states, some phylogeny building models allow the use of continuous characters so PC scores can be added to the model to encompass the entirety of shape change. Additionally a clustering analysis can be used to allocate species in to a predetermined number of groups based on their PC scores. Clustering methods can incorporate any number of PC scores so they can include more than one direction of shape change.

Fortuny et al. (2011, 2014, 2017) made some excellent progress in the biomechanical understanding of stereospondyl skulls, using some select species as examples. In

addition to this FEA work, basic bite biomechanics can be extracted from the lower jaw from simple linear measurements (Anderson et al., 2013). Linear measurements can be used to compare the posterior and anterior mechanical advantage, as well as the initial bite points (Anderson, 2013; Penrice and Ruta, 2017). The position of the mandible articulation (with respect to the posterior margin of the skull) can inform bite size (gape) and orientation as the effect of its variation in extant amphibians is well established (Trueb, 1993). These are useful bite performance metrics that do not need intact teeth to determine differences in bite capabilities. More advanced biomechanics, such as the FEA methods used by Fortuny et al. (2011) can be rendered from 2D images. With the increased availability of 3D scanning and modelling technologies, more advanced morphological investigations could reveal more precise understanding of the complexities of the stereospondyl skull.

The present thesis serves as basis for understanding the greatest source of shape variation and where these shapes were most successful in the palaeoclimate. So in addition to FEA models, it is possible to build functional models of the entire skull and skeleton and to model the movement of stereospondyls in their environment. The aim of this would be to test the stress on the skeletons in different arrangements, and from this to determine the most likely arrangement and whether it was capable of walking and swimming. These reconstructions have been successful in establishing probable range of motion in extinct pterosaurs, felid mammals and birds (Cuff et al., 2015; Hutchinson et al., 2015), so there is no reason to believe it could not be applied to stereospondyls.

7.8 Conclusions

Stereospondyls were the most speciose group of early tetrapods and their morphological disparity makes them even more interesting. A clade wide analysis of the morphologies of stereospondyls here has shown the functional history of the whole group for the first time. Stereospondyl prey seeking behaviour capitalized their competitive advantage in their environments. The clade survived the biggest mass extinction of all time, repopulating Pangea from their Southern refuge. Aquatic ambush predators, terrestrial invertebrate eaters, piscivorous active swimmers were all present in various forms. Early Triassic species did not last for long in the fossil record,

they were replaced by more specialized forms in the Middle Triassic and the longer stereospondyls were established in a place, the more disparate they became. These specialized forms were the eventual downfall of the clade as they were unable to adapt to the niche extinctions of the Late Triassic and were unable to compete with the rising reptilian species.

This thesis has shown that the morphology of stereospondyls changed in a functionally informative manner over the lifetime of the clade. This is the first clade wide analysis of their palaeobiology and has shown the true diversity of these early amphibians.

References

- Abrams, P.A., 1998. High competition with low similarity and low competition with high similarity: exploitative and apparent competition in consumer-resource systems. *The American Naturalist*, 152(1), pp.114-128.
- Adler, P.B. and Drake, J.M., 2008. Environmental variation, stochastic extinction, and competitive coexistence. *The American Naturalist*, 172(5), pp.E186-E195.
- Algeo, T.J., Chen, Z.Q., Fraiser, M.L. and Twitchett, R.J., 2011. Terrestrial–marine teleconnections in the collapse and rebuilding of Early Triassic marine ecosystems. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 308(1), pp.1-11.
- Alroy, J., 1996. Constant extinction, constrained diversification, and uncoordinated stasis in North American mammals. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 127(1-4), pp.285-311.
- Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. *Austral ecology*, 26(1), pp.32-46.
- Anderson, P.S., Friedman, M. and Ruta, M., 2013. Late to the table: diversification of tetrapod mandibular biomechanics lagged behind the evolution of terrestriality.
- Bates, K.T. and Falkingham, P.L., 2012. Estimating maximum bite performance in *Tyrannosaurus rex* using multi-body dynamics. *Biology Letters*, p.rsbl20120056.
- Beard, C., 2002. East of Eden at the Paleocene/Eocene boundary. *Science*, 295(5562), pp.2028-2029.
- Benson, R.B. and Butler, R.J., 2011. Uncovering the diversification history of marine tetrapods: ecology influences the effect of geological sampling biases. *Geological Society, London, Special Publications*, 358(1), pp.191-208.
- Benson, R.B., Butler, R.J., Alroy, J., Mannion, P.D., Carrano, M.T. and Lloyd, G.T., 2016. Near-stasis in the long-term diversification of Mesozoic tetrapods. *PLoS biology*, 14(1), p.e1002359.
- Benton, M.J., 2008. How to find a dinosaur, and the role of synonymy in biodiversity studies. *Paleobiology*, 34(4), pp.516-533.

- Benton, M.J., 2015. Exploring macroevolution using modern and fossil data. *Proceedings of the Royal Society B* (Vol. 282, No. 1810, p. 20150569).
- Benton, M.J. and Newell, A.J., 2014. Impacts of global warming on Permo-Triassic terrestrial ecosystems. *Gondwana Research*, 25(4), pp.1308-1337.
- Benton, M.J. and Pearson, P.N., 2001. Speciation in the fossil record. *Trends in Ecology & Evolution*, 16(7), pp.405-411.
- Benton, M.J., Tverdokhlebov, V.P. and Surkov, M.V., 2004. Ecosystem remodelling among vertebrates at the Permian–Triassic boundary in Russia. *Nature*, 432(7013), pp.97-100.
- Benton, M.J., Ruta, M., Dunhill, A.M. and Sakamoto, M., 2013. The first half of tetrapod evolution, sampling proxies, and fossil record quality. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 372, pp.18-41.
- Bolt, J.R. and Chatterjee, S., 2000. A new temnospondyl amphibian from the Late Triassic of Texas. *Journal of Paleontology*, 74(4), pp.670-683.
- Bona, P. and Desojo, J.B., 2011. Osteology and cranial musculature of *Caiman latirostris* (Crocodylia: Alligatoridae). *Journal of Morphology*, 272(7), pp.780-795.
- Bonett, R.M., Chippindale, P.T., Moler, P.E., Van Devender, R.W. and Wake, D.B., 2009. Evolution of gigantism in amphiumid salamanders. *PLoS one*, 4(5), p.e5615.
- Bonnan, M.F., 2007. Linear and geometric morphometric analysis of long bone scaling patterns in Jurassic neosauropod dinosaurs: their functional and paleobiological implications. *The Anatomical Record*, 290(9), pp.1089-1111.
- Botha-Brink, J., Codron, D., Huttenlocker, A.K., Angielczyk, K.D. and Ruta, M., 2016. Breeding young as a survival strategy during Earth's greatest mass extinction. *Scientific reports*, 6, p.24053.
- Bouetel, Virginie. (2005). Phylogenetic implications of skull structure and feeding behavior in balaenopterids (Cetacea, Mysticeti). *Journal of Mammalogy* 86.1 (2005): 139-146.
- Boy, J.A., 1977. Typen und Genese jungpaläozoischer Tetrapoden-Lagerstätten. *Palaeontographica Abteilung A*, pp.111-167.
- Brusatte, S.L., Butler, R.J., Mateus, O. and Steyer, J.S., 2015. A new species of *Metoposaurus* from the Late Triassic of Portugal and comments on the systematics and biogeography

- of metoposaurid temnospondyls. *Journal of Vertebrate Paleontology*, 35(3), p.e912988.
- Burton, R.F., 2008. The scaling of eye size in adult birds: relationship to brain, head and body sizes. *Vision research*, 48(22), pp.2345-2351.
- Canoville, A. and Chinsamy, A., 2015. Bone microstructure of the stereospondyl *Lydekkerina Huxleyi* reveals adaptive strategies to the harsh post permian-extinction environment. *The Anatomical Record*, 298(7), pp.1237-1254.
- Cardillo, M., Mace, G.M., Gittleman, J.L., Jones, K.E., Bielby, J. and Purvis, A., 2008. The predictability of extinction: biological and external correlates of decline in mammals. *Proceedings of the Royal Society of London B: Biological Sciences*, 275(1641), pp.1441-1448.
- Carlquist, S., 1966. The biota of long-distance dispersal. V. Plant dispersal to Pacific Islands. *Bulletin of the Torrey Botanical Club*, pp.129-162.
- Carroll, R.L. and Holmes, R., 1980. The skull and jaw musculature as guides to the ancestry of salamanders. *Zoological Journal of the Linnean Society*, 68(1), pp.1-40.
- de Souza Carvalho, I., de Gasparini, Z.B., Salgado, L., de Vasconcellos, F.M. and da Silva Marinho, T., 2010. Climate's role in the distribution of the Cretaceous terrestrial Crocodyliformes throughout Gondwana. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 297(2), pp.252-262.
- Chinsamy-Turan, A., 2005. *The microstructure of dinosaur bone: deciphering biology with fine-scale techniques*. John Wiley & Sons.
- Cirilli, S., Marzoli, A., Tanner, L., Bertrand, H., Buratti, N., Jourdan, F., Bellieni, G., Kontak, D. and Renne, P.R., 2009. Latest Triassic onset of the Central Atlantic magmatic province (CAMP) volcanism in the Fundy basin (Nova Scotia): new stratigraphic constraints. *Earth and Planetary Science Letters*, 286(3), pp.514-525.
- Clack, J.A., 2012. *Gaining ground: the origin and evolution of tetrapods*. Indiana University Press.
- Clapham, M.E. and Payne, J.L., 2011. Acidification, anoxia, and extinction: A multiple logistic regression analysis of extinction selectivity during the Middle and Late Permian. *Geology*, 39(11), pp.1059-1062.

- Clarke, K.R., 1993. Non-parametric multivariate analyses of changes in community structure. *Austral Ecology*, 18(1), pp.117-143.
- Clemente-Carvalho, R.B.G., Monteiro, L.R., Bonato, V., Rocha, H.S., Pereira, G.R., Oliveira, D.F., Lopes, R.T., Haddad, C.F.B., Martins, E.G. and Dos Reis, S.F., 2008. Geographic variation in cranial shape in the pumpkin toadlet (*Brachycephalus ephippium*): a geometric analysis. *Journal of Herpetology*, 42(1), pp.176-185.
- Cohen, K.M., Finney, S.C., Gibbard, P.L. & Fan, J.-X., 2014. The ICS International Chronostratigraphic Chart. Episodes 36: 199-204.
- Cosgriff, J.W. and DeFauw, S.L., 1987. A capitosaurid labyrinthodont from the Early Scythian of Tasmania. *Alcheringa*, 11(1), pp.21-41.
- Cosgriff, J.W. and Zawiskie, J.M., 1979. A new species of the Rhytidosteidae from the Lystrosaurus Zone and a review of the Rhytidosteoidea. *Palaeontologia Africana* 22: 1-27
- Cuff, A.R., Randau, M., Head, J., Hutchinson, J.R., Pierce, S.E. and Goswami, A., 2015. Big cat, small cat: reconstructing body size evolution in living and extinct Felidae. *Journal of Evolutionary Biology*, 28(8), pp.1516-1525.
- Curtis, N., Jones, M.E., Lappin, A.K., O'Higgins, P., Evans, S.E. and Fagan, M.J., 2010. Comparison between in vivo and theoretical bite performance: using multi-body modelling to predict muscle and bite forces in a reptile skull. *Journal of Biomechanics*, 43(14), pp.2804-2809.
- Damiani, R.J., 2000. Bone histology of some Australian Triassic temnospondyl amphibians: preliminary data. New York : Gordon and Breach Science Publishers
- Damiani, R.J., 2001. A systematic revision and phylogenetic analysis of Triassic mastodonsauroids (Temnospondyli: Stereospondyli). *Zoological Journal of the Linnean Society*, 133(4), pp.379-482.
- Damiani, R.J., 2004. Temnospondyls from the Beaufort Group (Karoo Basin) of South Africa and their biostratigraphy. *Gondwana Research*, 7(1), pp.165-173.
- Damiani, R.J. and Kitching, J.W., 2003. A new brachyopid temnospondyl from the *Cynognathus* Assemblage Zone, Upper Beaufort Group, South Africa. *Journal of Vertebrate Paleontology*, 23(1), pp.67-78.

- Damiani, R.J. and Warren, A., 1996. A new look at members of the Superfamily Brachyopoidea (Amphibia, Temnospondyli) from the Early Triassic of Queensland and a preliminary analysis of brachyopoid relationships. *Alcheringa*, 20(4), pp.277-300.
- Damiani, R.J. and Yates, A.M., 2003. The Triassic amphibian *Thoosuchus yakovlevi* and the relationships of the Trematosauroida (Temnospondyli: Stereospondyli). *Records-Australian Museum*, 55(3), pp.331-342.
- Damiani, R., Schoch, R.R., Hellrung, H., Werneburg, R. and Gastou, S., 2009. The plagiosaurid temnospondyl *Plagiosuchus pustuliferus* (Amphibia: Temnospondyli) from the Middle Triassic of Germany: anatomy and functional morphology of the skull. *Zoological Journal of the Linnean Society*, 155(2), pp.348-373.
- Deban, S.M. and Wake, D.B., 2000. Aquatic feeding in salamanders. pp.65-94 In *Feeding: form, function and evolution in tetrapod vertebrates*, Ed. K. Schwenk. Oxford. Elsevier
- Deban, S.M., O'Reilly, J.C. and Nishikawa, K.C., 2001. The evolution of the motor control of feeding in amphibians. *American Zoologist*, 41(6), pp.1280-1298.
- Deeming, D.C. and Ruta, M., 2014. Egg shape changes at the theropod–bird transition, and a morphometric study of amniote eggs. *Royal Society Open Science*, 1(3), p.140311.
- Defauw, S.L., 1989. Temnospondyl amphibians: a new perspective on the last phases in the evolution of the Labyrinthodontia. *Michigan Academician*, 21, pp.7-32.
- Dias-da-Silva, S. and Marsicano, C., 2011. Phylogenetic reappraisal of Rhytidosteidae (Stereospondyli: Trematosauria), temnospondyl amphibians from the Permian and Triassic. *Journal of Systematic Palaeontology*, 9(2), pp.305-325.
- Dias-da-Silva S., Marsicano, C. and Schultz, C.L., 2006. Rhytidosteid temnospondyls in Gondwana: a new taxon from the Lower Triassic of Brazil. *Palaeontology*, 49(2), pp.381-390.
- Dlugokencky, E., 2016. Annual mean carbon dioxide data. Earth System Research Laboratory. National Oceanic & Atmospheric Administration. Retrieved 12 February 2016.
- Drake, J.M. and Lodge, D.M., 2004. Effects of environmental variation on extinction and establishment. *Ecology Letters*, 7(1), pp.26-30.

- Erickson, G.M., Gignac, P.M., Stepan, S.J., Lappin, A.K., Vliet, K.A., Bruegggen, J.D., Inouye, B.D., Kledzik, D. and Webb, G.J., 2012. Insights into the ecology and evolutionary success of crocodilians revealed through bite-force and tooth-pressure experimentation. *PLoS One*, 7(3), p.e31781.
- Erwin, D.H., 2007. Disparity: morphological pattern and developmental context. *Palaeontology*, 50(1), pp.57-73.
- Escoriza, D. and Hassine, J.B., 2014. Phenotypic variability in larvae of two species of Mediterranean spadefoot toad: an approach using linear and geometric morphometrics. *African Journal of Herpetology*, 63(2), pp.152-165.
- Evans, A.R., Wilson, G.P., Fortelius, M. and Jernvall, J., 2007. High-level similarity of dentitions in carnivorans and rodents. *Nature*, 445(7123), pp.78-81.
- Ewert, J.P., 2004. Motion perception shapes the visual world of amphibians. In *Complex worlds from simpler nervous systems*, pp.117-160. Ed. F. Prete, USA, MIT Press
- Fabrezi, M. and Emerson, S.B., 2003. Parallelism and convergence in anuran fangs. *Journal of Zoology*, 260(1), pp.41-51.
- Fawcett, P.J., Barron, E.J., Robinson, V.D., Katz, B.J., 1994. The climatic evolution of India and Australia from the Late Permian to Mid-Jurassic: a comparison of climate model results with the geologic record. In: Klein, G.D. (Ed.), *Pangea: Paleoclimate, Tectonics and Sedimentation During Accretion, Zenith and Break-up of a Supercontinent*. Geol. Soc. Am. Spec. Paper, vol. 288, pp. 139–157
- Fortuny, J., Galobart, À. and De Santisteban, C., 2010. A new capitosaur from the Middle Triassic of Spain and the relationships within the Capitosauria. *Acta Palaeontologica Polonica*, 56(3), pp.553-566.
- Fortuny, J., Marce-Nogue, J., De Esteban-Trivigno, S., Gil, L. and Galobart, À., 2011. Temnospondyli bite club: ecomorphological patterns of the most diverse group of early tetrapods. *Journal of Evolutionary Biology*, 24(9), pp.2040-2054.
- Fortuny, J., Steyer, J.S. and Hoşgör, I., 2015. First occurrence of temnospondyls from the Permian and Triassic of Turkey: Paleoenvironmental and paleobiogeographic implications. *Comptes Rendus Palevol*, 14(4), pp.281-289.

- Fortuny, J., Marcé-Nogué, J., Steyer, J.S., de Esteban-Trivigno, S., Mújal, E. and Gil, L., 2016. Comparative 3D analyses and palaeoecology of giant early amphibians (Temnospondyli: Stereospondyli). *Scientific Reports*, 6, p.30387.
- Fortuny, J., Marcé-Nogué, J. and Konietzko-Meier, D., 2017. Feeding biomechanics of Late Triassic metoposaurids (Amphibia: Temnospondyli): a 3D finite element analysis approach. *Journal of Anatomy*, 230(6), pp.752-765.
- Fröbisch, N.B., Olori, J.C., Schoch, R.R. and Witzmann, F., 2010, June. Amphibian development in the fossil record. In *Seminars in cell & developmental biology* (Vol. 21, No. 4, pp. 424-431). Academic Press.
- Garamszegi, L.Z., Møller, A.P. and Erritzøe, J., 2002. Coevolving avian eye size and brain size in relation to prey capture and nocturnality. *Proceedings of the Royal Society of London B: Biological Sciences*, 269(1494), pp.961-967.
- Gardner, J.L., Peters, A., Kearney, M.R., Joseph, L. and Heinsohn, R., 2011. Declining body size: a third universal response to warming?. *Trends in Ecology & Evolution*, 26(6), pp.285-291.
- George, D. and Blicek, A., 2011. Rise of the earliest tetrapods: an early Devonian origin from marine environment. *PLoS One*, 6(7), p.e22136.
- Georgiev, S., Stein, H.J., Hannah, J.L., Bingen, B., Weiss, H.M. and Piasecki, S., 2011. Hot acidic Late Permian seas stifle life in record time. *Earth and Planetary Science Letters*, 310(3), pp.389-400.
- Gmelin, J.F. 1789. Caroli a Linné Systema naturae. 13. ed., Tom 1 Pars 3. G. E. Beer, Lipsiae. 1033-1516 pp.
- Goldfuss, A., 1847. *Beiträge zur vorweltlichen Fauna des Steinkohlengebirges*. In Commission bei Henry & Cohen.
- Grigg, G. and Kirshner, V., 2015. *Biology and evolution of crocodylians*. Csiro Publishing.
- Hall, M.I. and Ross, C.F., 2007. Eye shape and activity pattern in birds. *Journal of Zoology*, 271(4), pp.437-444.
- Hammer, Ø., Harper, D.A.T. and Ryan, P.D., 2001. Paleontological statistics software: Package for education and data analysis. *Palaeontologia Electronica*, (4).

- Harris, J.D., Lucas, S.G., Speilmann, J.A., Lockley, M.G., Milner, A.R. and Kirkland, J.I. eds., 2006. *The Triassic-Jurassic Terrestrial Transition: 37* (Vol. 37). New Mexico Museum of Natural History and Science.
- Heesy, C.P., 2004. On the relationship between orbit orientation and binocular visual field overlap in mammals. *The Anatomical Record*, 281(1), pp.1104-1110.
- Herrel, A., O'reilly, J.C. and Richmond, A.M., 2002. Evolution of bite performance in turtles. *Journal of Evolutionary Biology*, 15(6), pp.1083-1094.
- Hetherington, A.J., Sherratt, E., Ruta, M., Wilkinson, M., Deline, B. and Donoghue, P.C., 2015. Do cladistic and morphometric data capture common patterns of morphological disparity? *Palaeontology*, 58(3), pp.393-399.
- Holm, S., 1979. A simple sequentially rejective multiple test procedure. *Scandinavian journal of statistics*, pp.65-70.
- Humphries, S. and Ruxton, G.D., 2002. Why did some ichthyosaurs have such large eyes? *Journal of Experimental Biology*, 205(4), pp.439-441.
- Hutchinson, J.R., Rankin, J.W., Rubenson, J., Rosenbluth, K.H., Siston, R.A. and Delp, S.L., 2015. Musculoskeletal modelling of an ostrich (*Struthio camelus*) pelvic limb: influence of limb orientation on muscular capacity during locomotion. *PeerJ*, 3, p.e1001.
- Irmis, R.B., Whiteside, J.H. and Kammerer, C.F., 2013. Non-biotic controls of observed diversity in the paleontologic record: An example from the Permo-Triassic Karoo Basin of South Africa. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 372, pp.62-77.
- Ivanović, A., Vukov, T.D., Džukić, G., Tomašević, N. and Kalezić, M.L., 2007. Ontogeny of skull size and shape changes within a framework of biphasic lifestyle: a case study in six *Triturus* species (Amphibia, Salamandridae). *Zoomorphology*, 126(3), pp.173-183.
- Ivanović, A., Sotiropoulos, K., Džukić, G. and Kalezić, M.L., 2009. Skull size and shape variation versus molecular phylogeny: a case study of alpine newts (*Mesotriton alpestris*, Salamandridae) from the Balkan Peninsula. *Zoomorphology*, 128(2), pp.157-167.

- Iwasaki, S.I., 2002. Evolution of the structure and function of the vertebrate tongue. *Journal of Anatomy*, 201(1), pp.1-13.
- Jaslow, C.R., 1990. Mechanical properties of cranial sutures. *Journal of Biomechanics*, 23(4), pp.313-321.
- Jeannot, A.M., Damiani, R. and Rubidge, B.S., 2006. Cranial anatomy of the Early Triassic stereospondyl *Lydekkerina huxleyi* (Tetrapoda: Temnospondyli) and the taxonomy of South African lydekkerinids. *Journal of Vertebrate Paleontology*, 26(4), pp.822-838.
- Jenkins Jr, F.A., Shubin, N.H., Gatesy, S.M. and Warren, A., 2008. *Gerrothorax pulcherrimus* from the Upper Triassic Fleming Fjord Formation of East Greenland and a reassessment of head lifting in temnospondyl feeding. *Journal of Vertebrate Paleontology*, 28(4), pp.935-950.
- Johnson, D., 2009. *The geology of Australia*. Cambridge University Press.
- Jordan, G.E. and Piel, W.H., 2008. PhyloWidget: web-based visualizations for the tree of life. *Bioinformatics*, 24(14), pp.1641-1642.
- Kardong, Kenneth V. 1995. *Vertebrates: comparative anatomy, function, evolution*. McGraw-Hill.
- Kathe, W., 1999. Comparative morphology and functional interpretation of the sutures in the dermal skull roof of temnospondyl amphibians. *Zoological Journal of the Linnean Society*, 126(1), pp.1-39.
- Kingsolver, J.G. and Huey, R.B., 2008. Size, temperature, and fitness: three rules. *Evolutionary Ecology Research*, 10(2), pp.251-268.
- Kirk, E.C., 2006. Effects of activity pattern on eye size and orbital aperture size in primates. *Journal of Human Evolution*, 51(2), pp.159-170.
- Klingenberg, C.P., 2011. MorphoJ: an integrated software package for geometric morphometrics. *Molecular Ecology Resources*, 11(2), pp.353-357.
- Konietzko-Meier, D. and Klein, N., 2013. Unique growth pattern of *Metoposaurus diagnosticus krasiejowensis* (Amphibia, Temnospondyli) from the Upper Triassic of Krasiejów, Poland. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 370, pp.145-157.

- Laffont, R., Firmat, C., Alibert, P., David, B., Montuire, S. and Saucède, T., 2011. Biodiversity and evolution in the light of morphometrics: From patterns to processes. *Comptes Rendus Palevol*, 10(2), pp.133-142.
- Laurin, M., Canoville, A. and Germain, D., 2011. Bone microanatomy and lifestyle: a descriptive approach. *Comptes Rendus Palevol*, 10(5), pp.381-402.
- Lautenschlager, S., Witzmann, F. and Werneburg, I., 2016. Palate anatomy and morphofunctional aspects of interpterygoid vacuities in temnospondyl cranial evolution. *The Science of Nature*, 103(9-10), p.79.
- Lighthill, M.J., 1969. Hydromechanics of aquatic animal propulsion. *Annual Review of Fluid Mechanics*, 1(1), pp.413-446.
- Liu, J., 2016. *Yuanansuchus maopingchangensis* sp. nov., the second capitosauroid temnospondyl from the Middle Triassic Badong Formation of Yuanan, Hubei, China. *PeerJ*, 4, p.e1903.
- Liu, J. and Wang, Y., 2005. The first complete mastodonsauroid skull from the Triassic of China: *Yuanansuchus laticeps* gen. et sp. nov. *Journal of Vertebrate Paleontology*, 25(3), pp.725-728.
- Lleonart, J., Salat, J. and Torres, G.J., 2000. Removing allometric effects of body size in morphological analysis. *Journal of Theoretical Biology*, 205(1), pp.85-93.
- Lloyd, G.T., Pearson, P.N., Young, J.R. and Smith, A.B., 2012. Sampling bias and the fossil record of planktonic foraminifera on land and in the deep sea. *Paleobiology*, 38(4), pp.569-584.
- Lucas, S.G., 2009. Timing and magnitude of tetrapod extinctions across the Permo-Triassic boundary. *Journal of Asian Earth Sciences*, 36(6), pp.491-502.
- Lucas, S.G. and Tanner, L.H., 2015. End-Triassic nonmarine biotic events. *Journal of Palaeogeography*, 4(4), pp.331-348.
- Lucas, S.G., Tanner, L.H., Kozur, H.W., Weems, R.E. and Heckert, A.B., 2012. The Late Triassic timescale: age and correlation of the Carnian–Norian boundary. *Earth-Science Reviews*, 114(1), pp.1-18.

- MacIver, M.A., Schmitz, L., Mugan, U., Murphey, T.D. and Mobley, C.D., 2017. Massive increase in visual range preceded the origin of terrestrial vertebrates. *Proceedings of the National Academy of Sciences*, 114(12), pp.E2375-E2384.
- Maganuco, S. and Pasini, G., 2009. A new specimen of trematosaurian temnospondyl from the Lower Triassic of NW Madagascar, with remarks on palatal anatomy and taxonomic affinities. *Atti Societ italiana Museo Civico di Storia Naturale Milano*, 150, pp.91-112.
- Maganuco, S., Pasini, G. and Auditore, M., 2014. A revision of the short-faced stereospondyls *Mahavisaurus dentatus* and *Lyrosaurus australis* from the Lower Triassic of Madagascar: cranial anatomy, ontogenetic remarks, palaeoecology and rhytidosteid phylogeny. *Atti Societ italiana Museo Civico di Storia Naturale Milano*, 39, pp.1-64.
- Maisch, M.W., Matzke, A.T. and Sun, G., 2004. A relict trematosauroid (Amphibia: Temnospondyli) from the Middle Jurassic of the Junggar Basin (NW China). *Naturwissenschaften*, 91(12), pp.589-593.
- Mannion, P.D. and Upchurch, P., 2011. A re-evaluation of the ‘mid-Cretaceous sauropod hiatus’ and the impact of uneven sampling of the fossil record on patterns of regional dinosaur extinction. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 299(3), pp.529-540.
- Marcé-Nogué, J., Fortuny, J., De Esteban-Trivigno, S., Sánchez, M., Gil, L. and Galobart, À., 2015. 3D Computational mechanics elucidate the evolutionary implications of orbit position and size diversity of early amphibians. *PloS one*, 10(6), p.e0131320.
- Marjanović, D. and Laurin, M., 2007. Fossils, molecules, divergence times, and the origin of lissamphibians. *Systematic Biology*, 56(3), pp.369-388.
- Marjanović, D. and Laurin, M., 2009. The origins of modern amphibians: a commentary. *Evolutionary Biology*, 36(3), pp.336-338.
- Marsicano, C.A., 1999. Chigutisaurid amphibians from the Upper Triassic of Argentina and their phylogenetic relationships. *Palaeontology*, 42(3), pp.545-565.
- McBrayer, L.D., 2004. The relationship between skull morphology, biting performance and foraging mode in Kalahari lacertid lizards. *Zoological Journal of the Linnean Society*, 140(3), pp.403-416.

- McGowan, A.J. and Smith, A.B., 2008. Are global Phanerozoic marine diversity curves truly global? A study of the relationship between regional rock records and global Phanerozoic marine diversity. *Paleobiology*, 34(1), pp.80-103.
- McHugh, J.B., 2015. Paleohistology of *Micropholis stowi* (Dissorophoidea) and *Lydekkerina huxleyi* (Lydekkerinidae) humeri from the Karoo Basin of South Africa, and implications for bone microstructure evolution in temnospondyl amphibians. *Journal of Vertebrate Paleontology*, 35(1), p.e902845.
- Metcalf, I., Nicoll, R.S., Willink, R., Ladjavadi, M. and Grice, K., 2013. Early Triassic (Induan–Olenekian) conodont biostratigraphy, global anoxia, carbon isotope excursions and environmental perturbations: New data from Western Australian Gondwana. *Gondwana Research*, 23(3), pp.1136-1150.
- Miller, E.L., Soloviev, A.V., Prokopiev, A.V., Toro, J., Harris, D., Kuzmichev, A.B. and Gehrels, G.E., 2013. Triassic river systems and the paleo-Pacific margin of northwestern Pangea. *Gondwana Research*, 23(4), pp.1631-1645.
- Modesto, S.P., Smith, R.M., Campione, N.E. and Reisz, R.R., 2011. The last “pelycosaur”: a varanopid synapsid from the *Pristerognathus* Assemblage Zone, Middle Permian of South Africa. *Naturwissenschaften*, 98(12), pp.1027-1034.
- Mora, C., Frazier, A.G., Longman, R.J., Dacks, R.S., Walton, M.M., Tong, E.J., Sanchez, J.J., Kaiser, L.R., Stender, Y.O., Anderson, J.M. and Ambrosino, C.M., 2013. The projected timing of climate departure from recent variability. *Nature*, 502(7470), pp.183-187.
- Morales, M. and Shishkin, M.A., 2002. A re-assessment of *Parotosuchus africanus* (Broom), a capitosauroid temnospondyl amphibian from the Triassic of South Africa. *Journal of Vertebrate Paleontology*, 22(1), pp.1-11.
- Müller, S., 1838. Waarnemingen over de Indische Krokodillen en Beschrijving van Eene Nieuwe Soort. (Observations of the Indonesian crocodiles and description of a new species). *Tijdschrift voor Natuurlijke Geschiedenis en Physiologie*, 5: 61- 87.
- Nakajima, Y. and Schoch, R.R., 2011. The first temnospondyl amphibian from Japan. *Journal of Vertebrate Paleontology*, 31(5), pp.1154-1157.
- Nicholson, D.B., Holroyd, P.A., Benson, R.B. and Barrett, P.M., 2015. Climate-mediated diversification of turtles in the Cretaceous. *Nature Communications*, 6.

- Nishikawa, K. and Schwenk, K. 2002. Ingestion in reptiles and amphibians. In: Encyclopedia of Life Sciences. John Wiley & Sons, Ltd.
- Nogueira, M.R., Peracchi, A.L. and Monteiro, L.R., 2009. Morphological correlates of bite force and diet in the skull and mandible of phyllostomid bats. *Functional Ecology*, 23(4), pp.715-723.
- Ochev, V.G., 1966. Systematics and phylogeny of capitosauroid labyrinthodonts. *Izdatel'stvo Saratovskogo Universiteta, Saratov*, 184, pp.73-87.
- Pacheco, C.P., Eltink, E., Müller, R.T. and Dias-da-Silva, S., 2017. A new Permian temnospondyl with Russian affinities from South America, the new family Konzhukoviidae, and the phylogenetic status of Archegosauroida. *Journal of Systematic Palaeontology*, 15(3), pp.241-256.
- Pawley, K. and Warren, A., 2005. A terrestrial stereospondyl from the Lower Triassic of South Africa: the postcranial skeleton of *Lydekkerina huxleyi* (Amphibia: Temnospondyli). *Palaeontology*, 48(2), pp.281-298.
- Pawley, K.A.T. and Warren, A., 2006. The appendicular skeleton of *Eryops megacephalus* Cope, 1877 (Temnospondyli: Eryopoidea) from the Lower Permian of North America. *Journal of Paleontology*, 80(3), pp.561-580.
- Pease, C.M., Lande, R. and Bull, J.J., 1989. A model of population growth, dispersal and evolution in a changing environment. *Ecology*, 70(6), pp.1657-1664.
- Penney, D. and Jepson, J.E., 2014. *Fossil insects: an introduction to Palaeoentomology*. Siri Scientific Press.
- Penrice, S. and Deeming, D.C. 2016. Morphometrics of Feeding Anatomy in stereospondyl amphibians. In: Geological Society of Australia & Kruse, P. D., (author.) & García-Bellido, Diego, (editor.) & Holmes, James D., (editor.) & Laurie, J. R., (editor.) et al. 2016, Palaeo Down Under 2 : Adelaide 11-15th July 2016, Canberra Association of Australasian Palaeontologists
- Penrice, S. and Deeming, D.C. (under review). Morphometrics of Feeding Anatomy in stereospondyl amphibians. *Australasian Palaeontological Memoirs*
- Penrice, S. and Ruta, M. 2017. In Mills, D. and Westgarth, C., Dog bites: a multidisciplinary perspective. Sheffield. 5M Publishing

- Pettigrew JD. 1986. The evolution of binocular vision. In: Pettigrew JD, Sanderson KJ, Levick WR, editors. *Visual neuroscience*. London: Cambridge University Press.
- Pierce, S.E., Angielczyk, K.D. and Rayfield, E.J., 2008. Patterns of morphospace occupation and mechanical performance in extant crocodilian skulls: a combined geometric morphometric and finite element modeling approach. *Journal of Morphology*, 269(7), pp.840-864.
- Piñeiro, G., Ramos, A. and Marsicano, C., 2012. A rhinesuchid-like temnospondyl from the Permo-Triassic of Uruguay. *Comptes Rendus Palevol*, 11(1), pp.65-78.
- Polly, P.D., Stayton, C.T., Dumont, E.R., Pierce, S.E., Rayfield, E.J. and Angielczyk, K.D., 2016. Combining geometric morphometrics and finite element analysis with evolutionary modeling: towards a synthesis. *Journal of Vertebrate Paleontology*, 36(4), p.e1111225.
- Prentice, K.C., Ruta, M. and Benton, M.J., 2011. Evolution of morphological disparity in pterosaurs. *Journal of Systematic Palaeontology*, 9(3), pp.337-353.
- Preto, N., Kustatscher, E. and Wignall, P.B., 2010. Triassic climates—state of the art and perspectives. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 290(1), pp.1-10.
- R Core Team. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>.
- Raup, D.M. and Sepkoski, J.J., 1982. Mass extinctions in the marine fossil record. *Science*, 215(4539), pp.1501-1503.
- Rayfield, E.J., 2004. Cranial mechanics and feeding in *Tyrannosaurus rex*. *Proceedings of the Royal Society of London B: Biological Sciences*, 271(1547), pp.1451-1459.
- Retallack, G.J., 2013. Permian and Triassic greenhouse crises. *Gondwana Research*, 24(1), pp.90-103.
- Reynolds, S.H., 1913. *The vertebrate skeleton*. University press.
- Rinehart, L.F. and Lucas, S.G., 2013. Tooth form and function in temnospondyl amphibians: relationship of shape to applied stress. *New Mexico Museum of Natural History Bulletin*, 61, pp.533-542.

- Rinehart, L.F., Lucas, S.G. and Schoch, R.R., 2015. *Eocyclotosaurus appetolatus*, a new cyclotosaurid amphibian from the Middle Triassic (Perovkan) Moenkopi Formation of New Mexico, USA. *Journal of Vertebrate Paleontology*, 35(3), p.e929140.
- Rohlf, F.J., 2006. tpsDig2, version 2.1. <http://life.bio.sunysb.edu/morph>.
- Ronce, O., 2007. How does it feel to be like a rolling stone? Ten questions about dispersal evolution. *Annual Review of Ecology Evolution and Systematics*, 38, pp.231-253.
- Roopnarine, P.D., Angielczyk, K.D., Wang, S.C. and Hertog, R., 2007. Trophic network models explain instability of Early Triassic terrestrial communities. *Proceedings of the Royal Society of London B: Biological Sciences*, 274(1622), pp.2077-2086.
- Roscher, M., Stordal, F. and Svensen, H., 2011. The effect of global warming and global cooling on the distribution of the latest Permian climate zones. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 309(3), pp.186-200.
- Ruta, M., Coates, M.I. and Quicke, D.L., 2003. Early tetrapod relationships revisited. *Biological Reviews*, 78(2), pp.251-345.
- Ruta, M., Pisani, D., Lloyd, G.T. and Benton, M.J., 2007. A supertree of Temnospondyli: cladogenetic patterns in the most species-rich group of early tetrapods. *Proceedings of the Royal Society of London B: Biological Sciences*, 274(1629), pp.3087-3095.
- Ruta, M., Cisneros, J.C., Liebrecht, T., Tsuji, L.A. and Mueller, J., 2011. Amniotes through major biological crises: faunal turnover among parareptiles and the end-Permian mass extinction. *Palaeontology*, 54(5), pp.1117-1137.
- Ruta, M., Angielczyk, K.D., Fröbisch, J. and Benton, M.J., 2013, October. Decoupling of morphological disparity and taxic diversity during the adaptive radiation of anomodont therapsids. In *Proceedings of the Royal Society B* (Vol. 280, No. 1768, p. 20131071).
- Sahney, S., Benton, M.J. and Falcon-Lang, H.J., 2010. Rainforest collapse triggered Carboniferous tetrapod diversification in Euramerica. *Geology*, 38(12), pp.1079-1082.
- Sanchez, S., De Ploeg, G., Clément, G. and Ahlberg, P.E., 2010. A new tool for determining degrees of mineralization in fossil amphibian skeletons: The example of the Late Palaeozoic branchiosaurid *Apateon* from the Autun Basin, France. *Comptes Rendus Palevol*, 9(6), pp.311-317.

- Schaerlaeken, V., Holanova, V., Boistel, R., Aerts, P., Velensky, P., Rehak, I., Andrade, D.V. and Herrel, A., 2012. Built to bite: feeding kinematics, bite forces, and head shape of a specialized durophagous lizard, *Dracaena guianensis* (Teiidae). *Journal of Experimental Zoology Part A: Ecological Genetics and Physiology*, 317(6), pp.371-381.
- Schneider, C.A., Rasband, W.S. and Eliceiri, K.W., 2012. NIH Image to ImageJ: 25 years of image analysis. *Nature Methods*, 9(7), pp.671-675.
- Schoch, R.R., 1999. *Comparative Osteology of Mastodonsaurus Giganteus (Jaeger, 1828) from the Middle Triassic (Lettenkeuper: Longobardian) of Germany (Baden-Württemberg, Bayern, Thüringen); with 4 Plates* (Doctoral dissertation, Staatl. Museum für Naturkunde).
- Schoch, R.R., 2000. The origin and intrarelationships of Triassic capitosaurid amphibians. *Palaeontology*, 43(4), pp.705-727.
- Schoch, R.R., 2002. The early formation of the skull in extant and Paleozoic amphibians. *Paleobiology*, 28(2), pp.278-296.
- Schoch, R.R., 2006. Skull ontogeny: developmental patterns of fishes conserved across major tetrapod clades. *Evolution & Development*, 8(6), pp.524-536.
- Schoch, R.R., 2008. The Capitosauria (Amphibia): characters, phylogeny, and stratigraphy. *Palaeodiversity*, 1, pp.189-226.
- Schoch, R.R., 2009. Evolution of life cycles in early amphibians. *Annual Review of Earth and Planetary Sciences*, 37, pp.135-162.
- Schoch, R.R., 2013. The evolution of major temnospondyl clades: an inclusive phylogenetic analysis. *Journal of Systematic Palaeontology*, 11(6), pp.673-705.
- Schoch, R.R., 2014. *Amphibian evolution: the life of early land vertebrates*. John Wiley & Sons.
- Schoch, R.R. and Milner, A.R., 2000. *Stereospondyli: Stem-Stereospondyli, Rhinesuchidae, Rhytidostea, Trematosauroida, Capitosauroida: with 106 Figures and 16 Plates*. F. Pfeil.
- Schoch, R.R. and Milner, A.R., 2004. Structure and implications of theories on the origin of lissamphibians. *Recent advances in the origin and early radiation of vertebrates*,

pp.345-377. Eds G. Fuentes, M. Wilson and R Cloutier. München : Verlag Dr. Friedrich Pfeil

- Schoch, R.R. and Witzmann, F., 2009. Osteology and relationships of the temnospondyl genus *Sclerocephalus*. *Zoological Journal of the Linnean Society*, 157(1), pp.135-168.
- Schoch, R.R., Fastnacht, M., Fichter, J. and Keller, T., 2007. Anatomy and relationships of the Triassic temnospondyl *Sclerothorax*. *Acta Palaeontologica Polonica*, 52(1).
- Schoch, R.R., Milner, A.R. and Witzmann, F., 2014. Skull morphology and phylogenetic relationships of a new Middle Triassic plagiosaurid temnospondyl from Germany, and the evolution of plagiosaurid eyes. *Palaeontology*, 57(5), pp.1045-1058.
- Scotese, C. R., 2001. Atlas of Earth History, Volume 1, Paleogeography, PALEOMAP Project, Arlington, Texas, 52 pp.
- Sellers, K.C., Middleton, K.M., Davis, J.L. and Holliday, C.M., 2017. Ontogeny of bite force in a validated biomechanical model of the American alligator. *Journal of Experimental Biology*, 220(11), pp.2036-2046.
- Sengupta, D.P., 2003. Triassic temnospondyls of the Pranhita–Godavari basin, India. *Journal of Asian Earth Sciences*, 21(6), pp.655-662.
- Sheridan, J.A. and Bickford, D., 2011. Shrinking body size as an ecological response to climate change. *Nature Climate Change*, 1(8), pp.401-406.
- Sherratt, E., Gower, D.J., Klingenberg, C.P. and Wilkinson, M., 2014. Evolution of cranial shape in caecilians (Amphibia: Gymnophiona). *Evolutionary Biology*, 41(4), pp.528-545.
- Shishkin, M.A., Sennikov, A.G., Novikov, I.V. and Ilyina, N.V., 2006. Differentiation of tetrapod communities and some aspects of biotic events in the Early Triassic of Eastern Europe. *Paleontological Journal*, 40(1), pp.1-10.
- Smith, R.J., 2002. Estimation of body mass in paleontology. *Journal of Human Evolution*, 43(2), pp.271-287.
- Smith, R.M. and Botha-Brink, J., 2011. Morphology and composition of bone-bearing coprolites from the Late Permian Beaufort Group, Karoo Basin, South Africa. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 312(1), pp.40-53.

- Stayton, C.T. and Ruta, M., 2006. Geometric morphometrics of the skull roof of stereospondyls (Amphibia: Temnospondyli). *Palaeontology*, 49(2), pp.307-337.
- Stebbins, R.C. and Cohen, N.W., 1995. *A natural history of amphibians*. Princeton University Press.
- Steen, M.C., 1938. On the Fossil Amphibia from the Gas Coal of Nýřrany and other Deposits in Czechoslovakia. *Journal of Zoology*, 108(2), pp.205-283.
- Steinhorsdottir, M., Jeram, A.J. and McElwain, J.C., 2011. Extremely elevated CO₂ concentrations at the Triassic/Jurassic boundary. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 308(3), pp.418-432.
- Stevens, K.A., 2006. Binocular vision in theropod dinosaurs. *Journal of Vertebrate Paleontology*, 26(2), pp.321-330.
- Steyer, J.S., 2001. *Ontogénie et phylogénie des stégocéphales temnospondyles et seymouriamorphes: implications paléobiologiques et paléoenvironnementales* (Doctoral dissertation, Paris, Muséum national d'histoire naturelle).
- Steyer, J.S., 2002. The first articulated trematosaur ‘amphibian’ from the Lower Triassic of Madagascar: implications for the phylogeny of the group. *Palaeontology*, 45(4), pp.771-793.
- Steyer, J.S., 2003. A revision of the early Triassic “capitosaurs” (Stegocephali, Stereospondyli) from Madagascar, with remarks on their comparative ontogeny. *Journal of Vertebrate Paleontology*, 23(3), pp.544-555
- Steyer, J.S., Laurin, M., Castanet, J. and De Ricqlès, A., 2004. First histological and skeletochronological data on temnospondyl growth: palaeoecological and palaeoclimatological implications. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 206(3), pp.193-201.
- Steyer, J.S., Boulay, M. and Lorrain, S., 2010. 3D external restorations of stegocephalian skulls using ZBrush: the renaissance of fossil amphibians. *Comptes Rendus Palevol*, 9(6), pp.463-470.
- Stocker, M. R. & Butler, R. J. 2013. Phytosauria. Geological Society, London, Special Publications 379, 91-117.

- Sues, H.D. and Schoch, R.R., 2012. Anatomy and phylogenetic relationships of *Calamops paludosus* (Temnospondyli, Stereospondyli) from the Triassic of the Newark Basin, Pennsylvania. *Journal of Vertebrate Paleontology*, 33(5), pp.1061-1070.
- Sulej, T., 2007. Osteology, variability, and evolution of *Metoposaurus*, a temnospondyl from the Late Triassic of Poland. *Palaeontologia Polonica*, 64, pp.29-139.
- Svenning, J.C., Gravel, D., Holt, R.D., Schurr, F.M., Thuiller, W., Münkemüller, T., Schiffers, K.H., Dullinger, S., Edwards, T.C., Hickler, T. and Higgins, S.I., 2014. The influence of interspecific interactions on species range expansion rates. *Ecography*, 37(12), pp.1198-1209.
- Tanner, L.H., Lucas, S.G. and Chapman, M.G., 2004. Assessing the record and causes of Late Triassic extinctions. *Earth-Science Reviews*, 65(1), pp.103-139.
- Taylor, M.A., 1987. How tetrapods feed in water: a functional analysis by paradigm. *Zoological Journal of the Linnean Society*, 91(2), pp.171-195.
- Thébault, E. and Loreau, M., 2005. Trophic interactions and the relationship between species diversity and ecosystem stability. *The American Naturalist*, 166(4), pp.E95-E114.
- Thorne, P.M., Ruta, M. and Benton, M.J., 2011. Resetting the evolution of marine reptiles at the Triassic-Jurassic boundary. *Proceedings of the National Academy of Sciences*, 108(20), pp.8339-8344.
- Tickle, P.G., Ennos, A.R., Lennox, L.E., Perry, S.F. and Codd, J.R., 2007. Functional significance of the uncinat processes in birds. *Journal of Experimental Biology*, 210(22), pp.3955-3961.
- Trueb, L., 1993. Patterns of diversity in the lissamphibian skull. *The skull*, 2, pp.255-343.
- Ultsch, G.R., 2012. Metabolism, gas exchange, and acid-base balance of giant salamanders. *Biological Reviews*, 87(3), pp.583-601.
- Vanhooydonck, B., Boistel, R., Fernandez, V. and Herrel, A., 2010. Push and bite: trade-offs between burrowing and biting in a burrowing skink (*Acontias percivali*). *Biological Journal of the Linnean Society*, 102(1), pp.91-99.
- Veilleux, C.C. and Kirk, E.C., 2014. Visual acuity in mammals: effects of eye size and ecology. *Brain, Behavior and Evolution*, 83(1), pp.43-53.

- Vitt, L.J. and Caldwell, J.P., 2013. *Herpetology: an introductory biology of amphibians and reptiles*. Academic Press.
- von Jäger, G.F., 1828. *Über die fossile reptilien: welche in Württemberg aufgefunden worden sind*. JB Metzler.
- Wainwright, P., Carroll, A.M., Collar, D.C., Day, S.W., Higham, T.E. and Holzman, R.A., 2007. Suction feeding mechanics, performance, and diversity in fishes. *Integrative and Comparative Biology*, 47(1), pp.96-106.
- Walmsley, C.W., Smits, P.D., Quayle, M.R., McCurry, M.R., Richards, H.S., Oldfield, C.C., Wroe, S., Clausen, P.D. and McHenry, C.R., 2013. Why the long face? The mechanics of mandibular symphysis proportions in crocodiles. *PLoS One*, 8(1), p.e53873.
- Ward, P.D., Montgomery, D.R. and Smith, R., 2000. Altered river morphology in South Africa related to the Permian-Triassic extinction. *Science*, 289(5485), pp.1740-1743.
- Warren, A., 1998. *Laidleria* uncovered: a redescription of *Laidleria gracilis* Kitching (1957), a temnospondyl from the Cynognathus Zone of South Africa. *Zoological Journal of the Linnean Society*, 122(1-2), pp.167-185.
- Warren, A. and Black, T., 1985. A new rhytidosteid (Amphibia, Labyrinthodontia) from the Early Triassic Arcadia Formation of Queensland, Australia, and the relationships of Triassic temnospondyls. *Journal of Vertebrate Paleontology*, 5(4), pp.303-327.
- Warren, A. and Hutchinson, M.N., 1983. The last labyrinthodont? A new brachyopoid (Amphibia, Temnospondyli) from the Early Jurassic Evergreen Formation of Queensland, Australia. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 303(1113), pp.1-62.
- Warren, A. and Marsicano, C., 2000. A phylogeny of the Brachyopoidea (Temnospondyli, Stereospondyli). *Journal of Vertebrate Paleontology*, 20(3), pp.462-483.
- Warren, A., Rich, T.H. and Vickers-Rich, P., 1997. The last last labyrinthodonts. *Palaeontographica Abteilung Stuttgart*, 247, pp.1-24.
- Warren, A., Damiani, R.J. and Yates, A.M., 2001. Palaeobiogeography of Australian fossil amphibians. *Historical Biology*, 15(1-2), pp.171-179.

- Warren, A., Rozefelds, A.C. and Bull, S., 2011. Tupilakosaur-like vertebrae in *Bothriceps australis*, an Australian brachyopid stereospondyl. *Journal of Vertebrate Paleontology*, 31(4), pp.738-753.
- Watson, D.M.S., 1919. The Structure, Evolution and Origin of the Amphibia. The "Orders" Rachitomi and Stereospondyli. *Philosophical Transactions of the Royal Society of London. Series B, Containing Papers of a Biological Character*, 209, pp.1-73.
- Watson, D.M.S., 1958. *A new labyrinthodont (Paracyclotosaurus) from the Upper Trias of New South Wales*. British Museum (Natural History).
- Wells, K.D., 2007. *The ecology and behavior of amphibians*. University of Chicago Press
- Werner, Y.L. and Seifan, T., 2006. Eye size in geckos: asymmetry, allometry, sexual dimorphism, and behavioral correlates. *Journal of Morphology*, 267(12), pp.1486-1500.
- Wilkinson, M., San Mauro, D., Sherratt, E. and Gower, D.J., 2011. A nine-family classification of caecilians (Amphibia: Gymnophiona). *Zootaxa*, 2874, pp.41-64.
- Witzmann, F., 2006. Developmental patterns and ossification sequence in the Permian-Carboniferous temnospondyl *Archegosaurus decheni* (Saar-Nahe Basin, Germany). *Journal of Vertebrate Paleontology*, 26(1), pp.7-17.
- Witzmann, F., 2007. The evolution of the scalation pattern in temnospondyl amphibians. *Zoological Journal of the Linnean Society*, 150(4), pp.815-834.
- Witzmann, F., 2016. CO₂-metabolism in early tetrapods revisited: inferences from osteological correlates of gills, skin and lung ventilation in the fossil record. *Lethaia*, 49(4), pp.492-506.
- Witzmann, F. and Schoch, R.R., 2006. The postcranium of *Archegosaurus decheni*, and a phylogenetic analysis of temnospondyl postcrania. *Palaeontology*, 49(6), pp.1211-1235.
- Witzmann, F. and Scholz, H., 2007. Morphometric study of allometric skull growth in the temnospondyl *Archegosaurus decheni* from the Permian/Carboniferous of Germany. *Geobios*, 40(4), pp.541-554.

- Witzmann, F., Scholz, H., Mueller, J. and Kardjilov, N., 2010. Sculpture and vascularization of dermal bones, and the implications for the physiology of basal tetrapods. *Zoological Journal of the Linnean Society*, 160(2), pp.302-340.
- Witzmann, F., Schoch, R.R., Hilger, A. and Kardjilov, N., 2012. Braincase, palatoquadrate and ear region of the plagiosaurid *Gerrothorax pulcherrimus* from the Middle Triassic of Germany. *Palaeontology*, 55(1), pp.31-50.
- Wold, S., Esbensen, K. and Geladi, P., 1987. Principal component analysis. *Chemometrics and Intelligent Laboratory Systems*, 2(1-3), pp.37-52.
- Yates, A.M., 1999. The Lapilopsidae: a new family of small temnospondyls from the Early Triassic of Australia. *Journal of Vertebrate Paleontology*, 19(2), pp.302-320.
- Yates, A.M. and Warren, A., 2000. The phylogeny of the 'higher' temnospondyls (Vertebrata: Choanata) and its implications for the monophyly and origins of the Stereospondyli. *Zoological Journal of the Linnean Society*, 128(1), pp.77-121.

Appendices

Word Count: The final word count is 56, 112 excluding references and appendices.

Electronic Appendix One:

List of stereospondyl species and their taxonomic groups

Electronic Appendix Two:

List of stereospondyl species used in the thesis

Electronic Appendix Three:

Labelled plots of morphospace occupation from chapter 4

Electronic Appendix Four:

List of extant amphibians used in the thesis